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COMPARATIVE STUDY of the GLOSSAE OF BEES (APOIDEA)

by

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ABSTRACT

Glossae of 290 species representing nearly all suprageneric taxa of bees, and many genera within some such taxa, were examined using the scanning electron microscope as well as cleared material under light microscopes. Emphasis was placed on apical structures. Homologies of various parts are postulated. Major features are an annulate, morphologically anterior surface bearing annular hairs and a disannulate, morphologically posterior surface bearing disannular hairs, most of which are seriate hairs (in two rows) except in Colletidae and Stenotritidae. In long-tongued bees the disannulate surface is invaginated and forms the glossal canal, in the wall of which is the glossal rod, which sometimes partly encloses the smaller bacular canal. In Colletidae the disannular surface is elaborated into the glossal lobes bearing the glossal brush; in long-tongued bees and some others it is elaborated into the flabellum. New characters usable at the family level are not numerous. One such is the presence of preapically bifid or modified annular hairs in Halictidae (except most Dufoureinae); such hairs do not occur in other families. Group characters are more numerous at subfamily, tribal, and generic levels. Examples are the bipartite flabella of Ctenioschelini, the transversely grooved serial ridges of Perdita and the coarsely cobblestoned but otherwise placoid flabella of the Eucerini. The similarity of meliponine, apine, and bombine glossae, all very different from those of euglossines, does not support the current classification of the Apidae. The tendency for reduced glossal complexity in parasitic bees suggests that part of the glossal attributes may be associated with nest construction and provisioning rather than feeding.

CONTENTS

INTRODUCTION

Mouthparts of bees have been extensively used in developing the current classification of these insects. Indeed some of the best familial characters are in the mouthparts, inconveniently hidden from easy examination in most dried specimens. The mouthparts, however, contain many interesting characters as yet unstudied. The investigation here reported concerns the glossa, the characteristics of which, both as seen by the light microscope and by the scanning electron microscope (SEM), are valuable for indicating relationships. There are also interesting convergences, especially among parasitic forms, that suggest the important roles that the glossa must perform.

ACKNOWLEDGEMENTS

We wish to thank Dr. Ronald J. McGinley for making the SEM photographs of glossae of colletid bees and, for comparative purposes, sphecoid wasps and other Hymenoptera. Brian H. Smith made some of the SEM photographs of other bees for us. (Most were made by Brooks.) All the SEM work was done at the Electron Microscope Facility of the University of Kansas with the help of Lorraine Hammer. For expert typing and editorial assistance we thank Joetta Weaver.

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MATERIALS AND METHODS

The proboscides have been examined for 290 species representing all families and subfamilies and nearly all tribes of the Apoidea. Those of various other Hymenoptera, especially sphecoid wasps, have also been studied. After separation from the head, for study with light microscopy, each proboscis was placed in a solution (about 10%) of sodium hydroxide (usually over night at room temperature) until all muscle tissue was dissolved or removable. It was then transferred to water acidulated with acetic acid for at least 10 minutes, and thence to glycerine in which the parts were permanently preserved. While still in water the proboscis was maximally extended by holding the prementum and gently pulling the glossa with a needle or fine forceps. Examination was with a binocular dissecting microscope and, for finer details, a compound microscope.

Proboscides of 176 species were examined and photographed with a Philips 501 SEM. The dry glossae were placed in warm water containing a little detergent (Triton-X) and cleaned in a three ounce ultrasonicator for about three minutes. They were then transferred to xylene, sonicated again, air dried, and attached with casein (Elmer's) glue to the stud for microscopy. Coating was with 200 Å of gold-palladium and scanning with 15 KV and 200 spot size. SEM photographs of colletids and sphecoid wasps made with the same instrument by Dr. R. J. McGinley (see McGinley, 1980) were also available and a few are reproduced here.

Cross-sectional views were obtained by cutting the cleared glossa (in glycerine), often two or three times, near the middle with a pair of fine scissors and examining the resultant short sections end on, with transmitted light, using dissecting and compound microscopes. This method is adequate for seeing the general shape, extent of the annulate surface, and shape of the glossal rod if present, but in long-tongued bees, especially small species, it is often difficult to determine the extent of the invaginated disannulate surface which is dotted in the diagrams.

The species studied are listed after the account of each taxon, with the notations C for cleared preparation and SEM for scanning electron micrograph. For practical reasons not all preparations and not all species were examined for every character listed in the descriptions. The SEM photographs were primarily of the apices of the glossae. Certain structures are better studied with SEM photographs than with cleared preparations while for other structures the reverse is the case. Good understanding of the structures can often be achieved only by using both methods.

MORPHOLOGY AND TERMINOLOGY

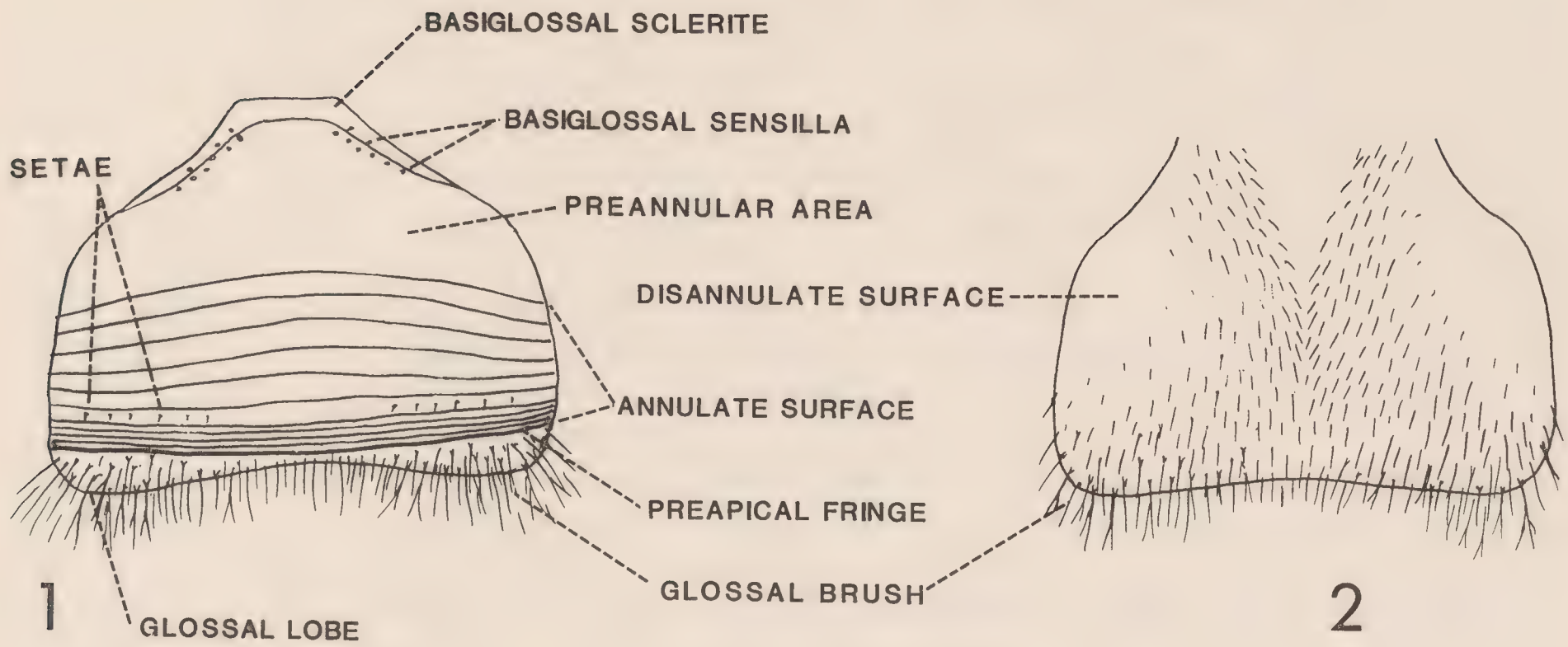
The terms used are based on those of Snodgrass (1956), McGinley (1980), and Winston (1979). New terms introduced here are marked with asterisks.

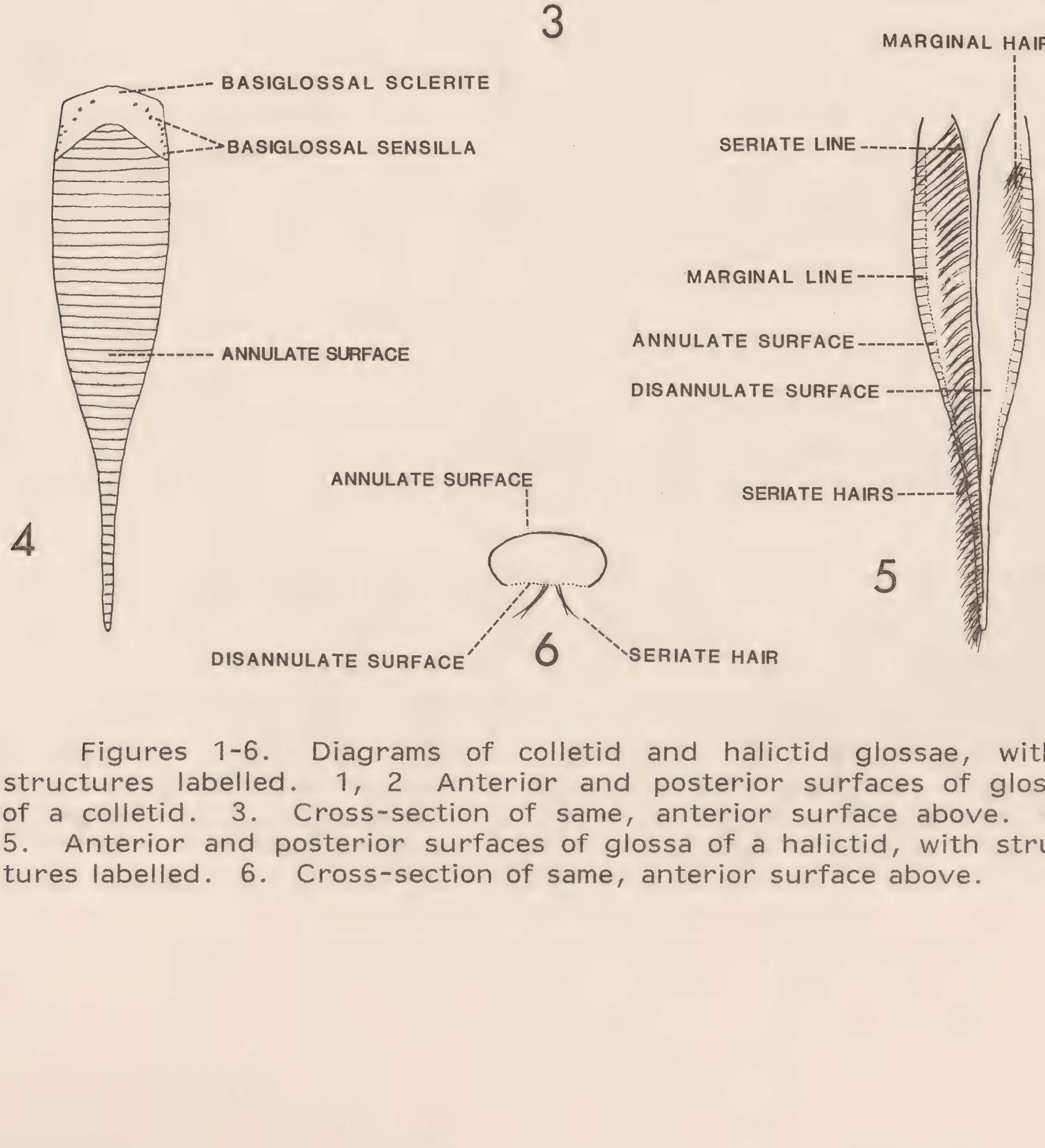
The proboscis is regarded as projecting downward from the head. Thus the anterior surface of the glossa is the surface that would be called dorsal if the proboscis were considered to project forward, and the posterior surface would be called ventral in that case.

Unlike most insects, there is only one "tongue" in the Hymenoptera. It is believed to be a fusion product of the two glossae of most insects (Snodgrass, 1935, 1956; Michener, 1944), and it is called the glossa. In most Hymenoptera other than bees it is a rather short, blunt, truncate, or commonly bilobed structure. It is at least superficially similarly truncate or bilobed in most members of the bee family Colletidae, but is pointed and often elongate and slender in most other bees. The parts of the glossa are labelled in Figures 1-10.

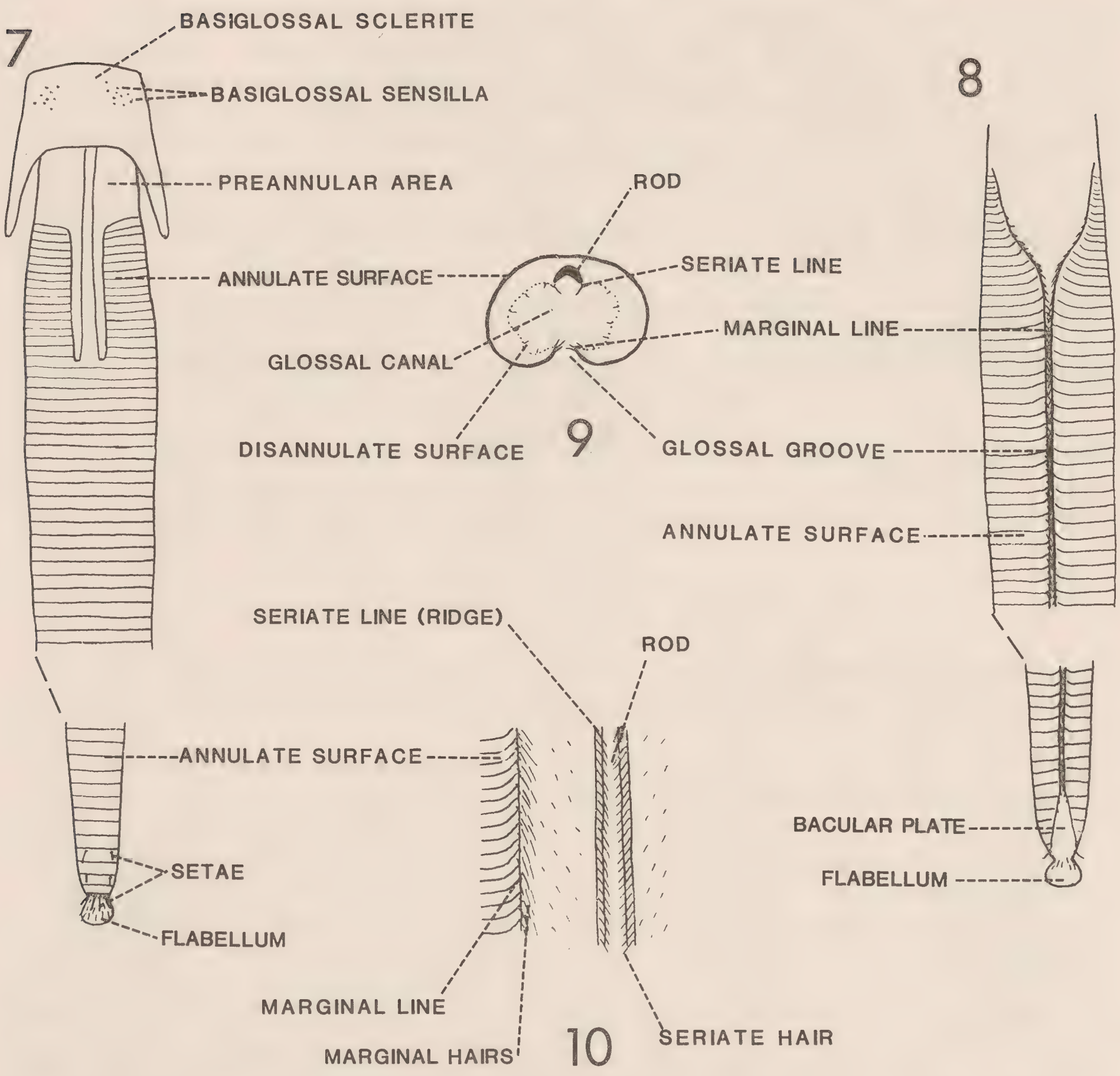
The anterior surface of the glossa bears transverse rows of hairs whose bases spread and commonly join laterally to form dark ridges. Because in long-tongued bees these ridges continue nearly all the way around the glossa, and are thus ringlike, they are termed annuli. The hairs arising from the annuli are annular hairs.* These hairs are not setae; they do not arise from sockets but are broadly attached to the annuli (Figs. 31A; 32E, H; 95E; 99A). They may be greatly enlarged spicules, similar to but larger than those found on various sclerites and especially membranes.

While the morphological anterior surface is largely or wholly annulate, in many bees there are modifications. For example, this surface may be expanded and the posterior surface invaginated so that the word anterior is not descriptive. For this reason the area covered with annuli is called the annulate surface.* It is homologous to the anterior surface of wasps, except that at the base of the anterior surface of the





Figures 1-6. Diagrams of colletid and halictid glossae, with structures labelled. 1, 2 Anterior and posterior surfaces of glossa of a colletid. 3. Cross-section of same, anterior surface above. 4, 5. Anterior and posterior surfaces of glossa of a halictid, with structures labelled. 6. Cross-section of same, anterior surface above.



Figures 7-10. Diagrams of the glossa of a long-tongued bee, with structures labelled. 7, 8. Anterior and posterior surfaces. 9. Cross-section of same, anterior surface above. 10. Inner surface of a portion of the glossal canal and adjacent edge of annulate surface, flattened out.

glossa is an area without annuli called the preannular area, basal to which is the basiglossal sclerite. In short-tongued bees, an irregular line of sensilla, the basiglossal sensilla, lies approximately along the line between the basiglossal sclerite and the preannular area. If the preannular area is somewhat sclerotized and joined to the basiglossal sclerite, as in Pseudaugochloropsis, the basiglossal sensilla seem to be in the middle of the basiglossal sclerite. In Ctenoplectra, various colletids, and others this line is broadly broken medially and in long-tongued bees as well as Diphaglossinae, the basiglossal sensilla are in two clusters, one on each side, on the basiglossal sclerite.

The morphological apex of the glossa is at the distal margin of the annulate surface, i.e., where the anterior and posterior surfaces meet distally. This statement is based on wasps and other Hymenoptera in which the annulate surface reaches the glossal apex. In Colletidae, however, the morphological apex is marked by a distinct transverse preapical fringe (Figs. 1, 11D), and is surpassed by the commonly bilobed extension of the posterior surface, called the glossal lobes, from which the glossal brush arises. The flabellum, when present in other families of bees, is also largely or wholly beyond the annulate surface and may be similar in derivation to the glossal lobes of colletids.

The morphological posterior surface of the glossa is bare, uniformly hairy, or with hairs in various patterns, but it lacks annuli. It is therefore called the disannulate surface.* The hairs on this surface, like the annular hairs, are not setae and do not arise from sockets (Figs. 31I; 32C, D, G; 38I; 52F; 59C; etc.); they are called the disannular hairs.* These hairs are exposed in most short-tongued bees but in long-tongued bees are mostly minute and largely hidden inside of the glossal canal which is formed by invagination of the disannulate surface.

In long-tongued bees the lateral margins of the annulate surface, instead of being on the lateral margins of the glossa, are drawn toward the median posterior line of the glossa, forming between them the glossal groove* (Fig. 8). The disannulate surface, in this case, is invaginated to form the glossal canal (Fig. 9), which extends for most of the length of the glossa but is open for its full length along the glossal groove. The glossal canal has also been called the salivary canal (Snodgrass, 1956).

In many bees the hairs along the lines (called marginal lines*) where the annulate and disannulate surfaces meet appear to be particularly dense. The marginal lines may be vague because in some bees the annuli fade away instead of ending sharply. The hairs arising near the marginal lines are called marginal hairs.* In short-tongued bees; they are usually prominent only near the base of the glossa. The name "marginal" seems particularly appropriate in long-tongued bees because they margin and tend to fill the glossal groove. In some long-tongued bees the annuli do not reach the glossal groove. This is probably because of reduction of the annuli in a zone on either side of the groove. The hairs along the lips of the groove are here termed marginal hairs, even though in this case they are not at the margin of the actually annulate surface.

The marginal hairs are not all alike. Some of them are annular hairs, often smaller but sometimes larger than other annular hairs. Marginal hairs may be especially dense because in some long-tongued bees the ends of the annuli bend basad so that the annuli are closer together in the marginal area than elsewhere. In long-tongued bees the hairs may appear dense when the glossa is viewed from the posterior surface because the margins of the annulate surface are often inflexed into the glossal groove (Figs. 63, 65, 76, etc.), so that the line of sight in this area is tangential to the surface or nearly so. Finally, disannular hairs are often involved. When they are similar in form and size to nearby annular hairs, and when the hairs are dense, it may be almost

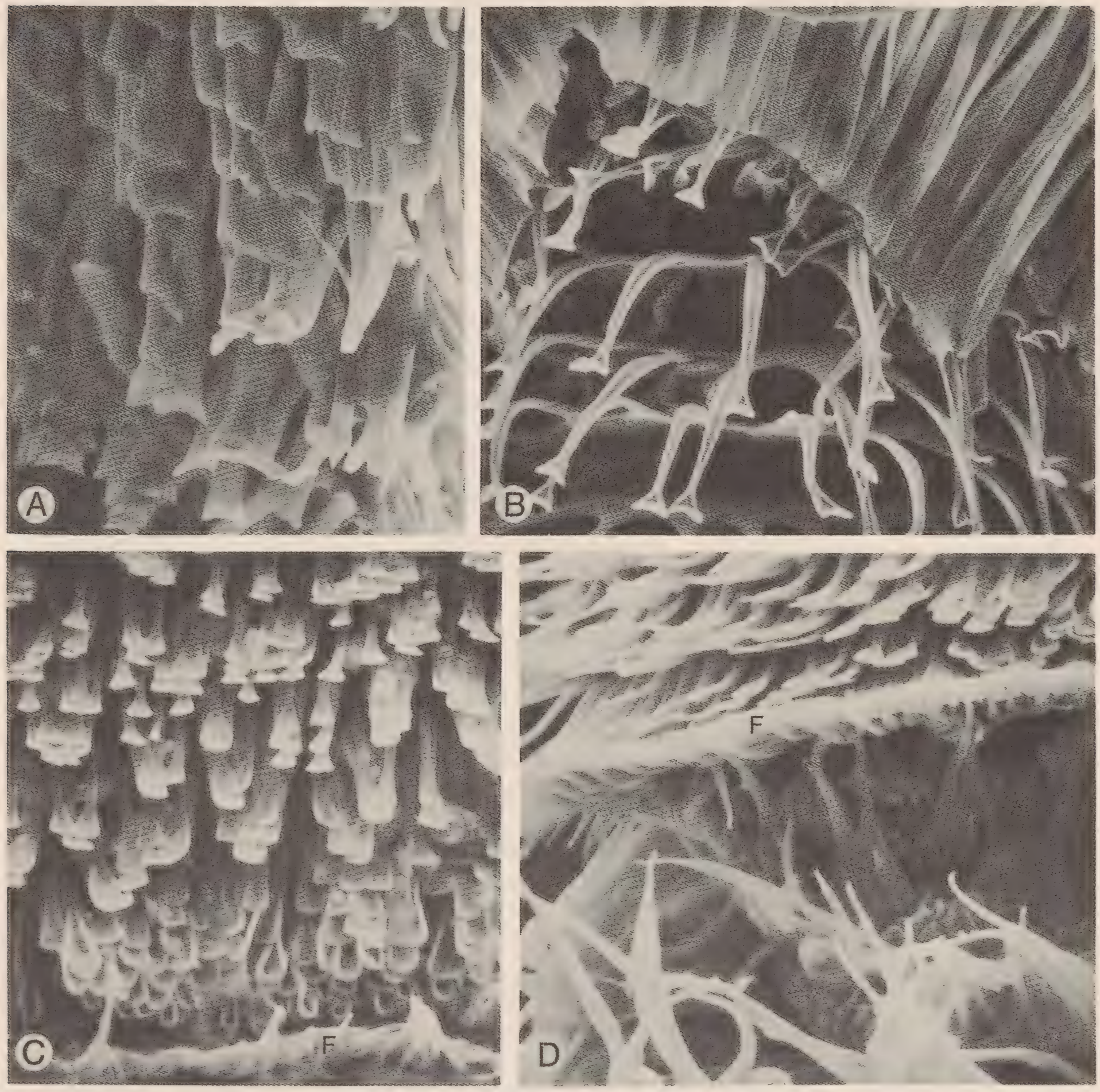


Figure 11. Hairs of anterior surfaces of sphecoid and colletid glossae (photographs by R. McGinley). Scale line = .01 mm, applies to all four photographs. A, Annular hairs of Philanthus ventrilabris. B, Annular hairs (near base of glossa) of Policana albopilosa. C, Annular hairs of Hylaeus episcopalis, preapical fringe (F) at lower margin. D, Hylaeus episcopalis; top to bottom: annular hairs, preapical fringe (F), and glossal lobe.

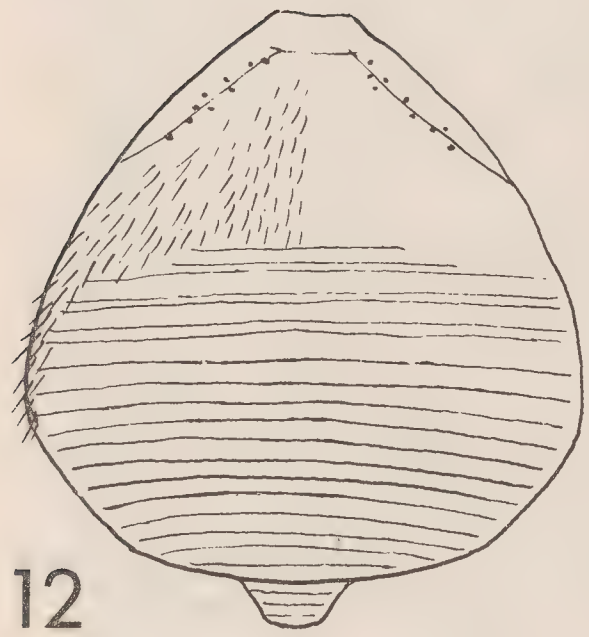
impossible to decide where the often weakened ends of the annuli are, especially if the margins of the annulate surface are inflexed. Thus the term marginal hairs may be only one of convenience, perhaps pertaining to dissimilar things, but its use is nonetheless practical.

In many bees the disannulate surface bears two longitudinal rows of hairs, running more or less from the base of the glossa, where the rows are well separated, to the distal region, where the rows are close

together or fused, sometimes diverging again just before the apex of the glossa. These are the seriate hairs.* In many bees these hairs are short and simple, but in some short-tongued bees they are enormous (the largest hairs on the glossa) and branched (Figs. 16; 26; 31E, I; 32B, etc.). In some bees which lack or nearly lack marginal hairs, the seriate hairs are very close to the margins of the annulate surface (Figs. 16, 43). In long-tongued bees the seriate hairs are minute (sometimes absent) and close to the glossal rod or on ridges (seriate lines) of the glossal rod (Figs. 9, 10, 62, etc.). Some bees in which the seriate hairs are limited, for example to the apex of the glossa, or which lack seriate hairs, nonetheless have a pair of lines or ridges to which the seriate hairs would be attached if they were present. Such lines or ridges, whether haired or not, are termed the seriate lines.* In short-tongued bees, if there are only two longitudinal lines on the posterior surface of the glossa, it is sometimes not easy to tell whether they are the seriate lines or the marginal lines. If one can follow such lines, commonly toward the apex of the glossa, to where each bears a row of often branched, seriate hairs, they are the seriate lines. If one can follow them, commonly toward the glossal base, to where each supports an area (rather than a row) of marginal hairs, then they are marginal lines. Of course the annuli should end along the marginal lines. Forms exist, like Pseudopanurgus aethiops (Fig. 45) and especially some Andrena (Fig. 43), in which the space between the marginal and seriate lines is only a narrow strip. And in some Andrena, except near the base of the glossa, the ends of the annuli appear to reach or nearly reach the seriate lines so that the seriate and marginal lines are fused.

The integument of the disannulate surface of short-tongued bees is frequently delicate and membranous (indicated by dotted lines in cross-sectional diagrams) but often the seriate hairs are on weak longitudinal ridges. This is especially true when the integument of the zone between the two rows of seriate hairs is slightly sclerotized. There are all degrees of such sclerotization, from that just sufficient to maintain the weak concavity of the surface between the rows of seriate hairs to that sufficiently strong that if one tears the glossal integument, this zone can be stripped from the rest of the glossa intact and often carrying the seriate hairs along its margins. When noticeable, this sclerotized zone, margined by the seriate hairs, is called the glossal thickening.*

In long-tongued bees the rows of seriate hairs are close together and the glossal thickening is usually intensified, forming the glossal rod (Figs. 9, 10, 62-91). This rod is often narrow, so that the seriate hairs are separated from the rod by unsclerotized integument (Figs. 70, 74, 81). Sometimes (e.g., in Megachilidae, Fig. 65) sclerotization along the ridges from which the seriate hairs arise forms a secondary rod on each side of the median rod proper, the seriate hairs arising from the secondary rods. Sometimes (e.g., in Apis, Fig. 89) the rod encompasses the whole space between the rows of seriate hairs, which therefore arise from lateral seriate ridges on the glossal rod itself. These ridges may be high and enclose a channel, the bacular canal,* which like the rod is on the anterior surface of the glossal canal, and like the latter is incompletely closed along its posterior surface



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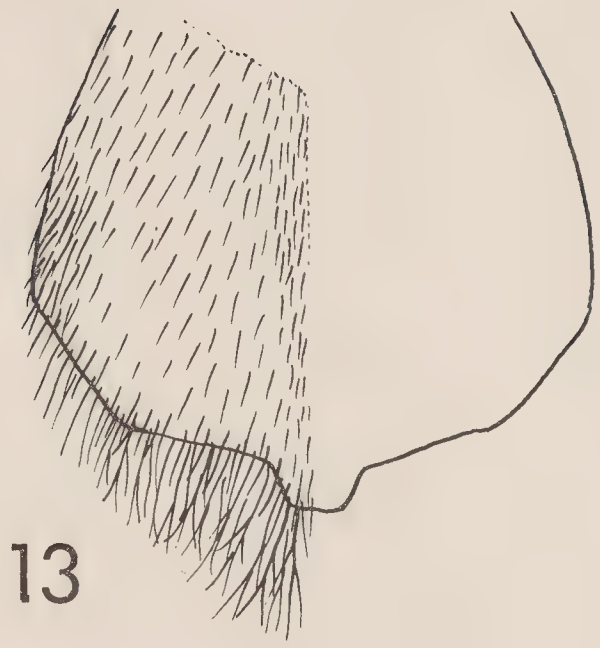

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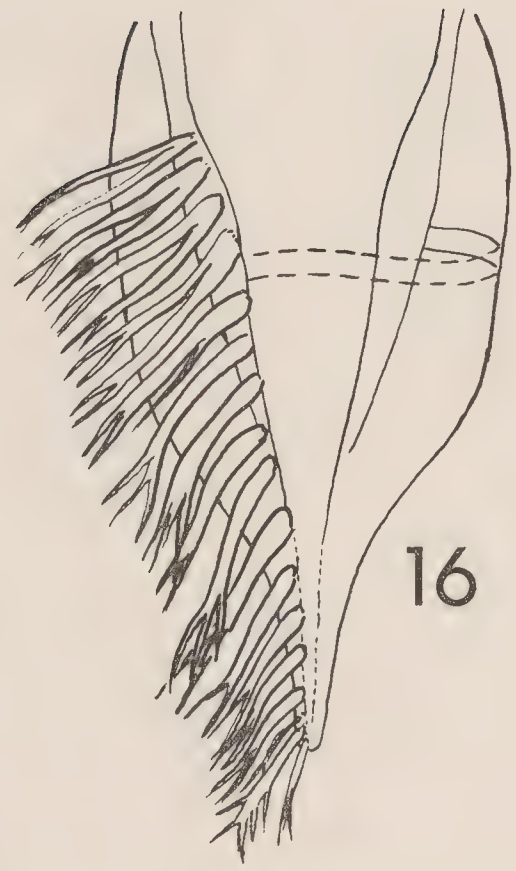

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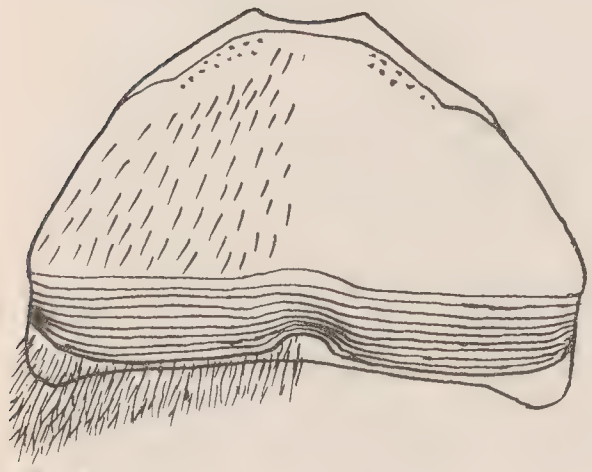

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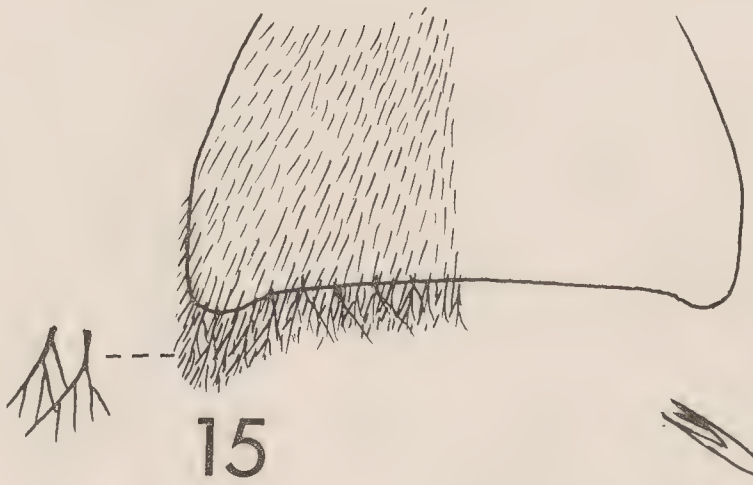

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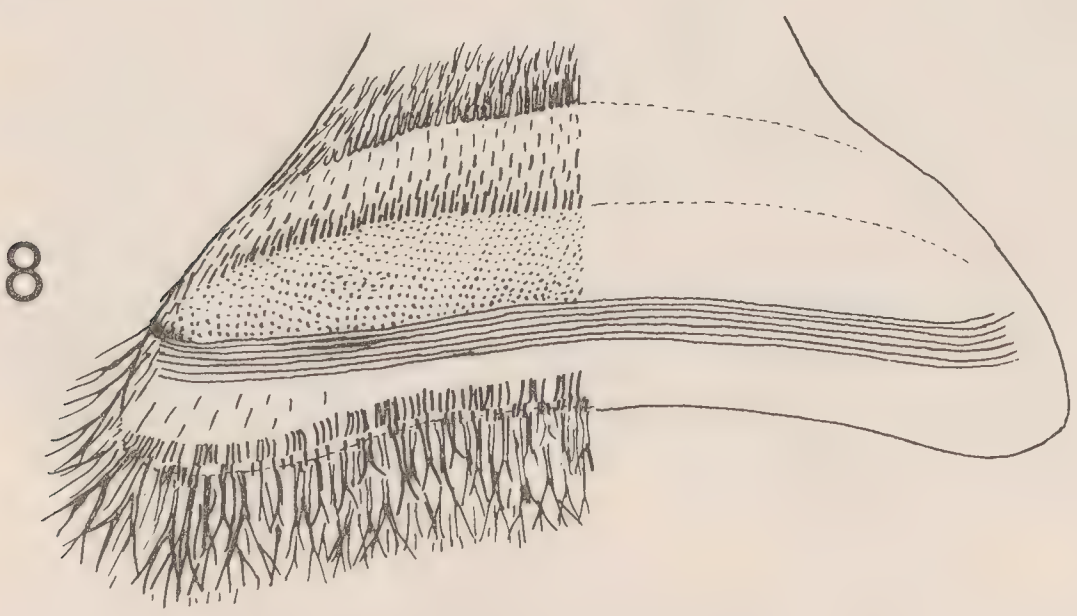

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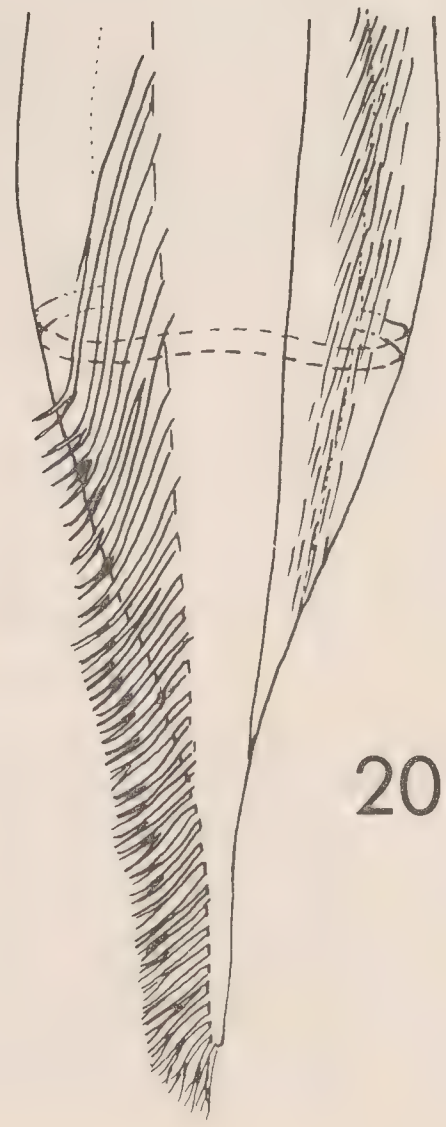

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Figure 21. Glossa and paraglossae of Meroglossa torrida, male, anterior view (photograph by R. McGinley).

(Figs. 76, 88, 99). The commonly converging seriate hairs partly close the bacular canal, as the marginal hairs partly close the glossal canal. In most Apidae the sclerotization (or at least darkening) of the rod is strongest laterally so that the rod appears double (Figs. 86-91).

Figures 12-20. Diagrams of colletid glossae. 12, 13. Anterior and posterior surfaces, Amphylaeus morosus, male. 14, 15. Same, female. 16. Posterior surface, Meroglossa torrida, male. 17. Cross-section of same. 18, 19. Anterior and posterior surfaces, Palaeorhiza parallela, female. 20. Posterior surface of same, male. The pair of transverse lines across a glossa (Figs. 16 and 20) represent two annuli, the lines being broken where they are on anterior surface. Annular hairs and other annuli are omitted. For Figure 17 the conventions are the same as for sectional diagrams, Figures 22-30.

At least in many dead long-tongued bees the median part of the glossal rod becomes evaginated, together with the rest of the disannulate surface, through the glossal groove (Figs. 65, 69, 72, 75, etc.). Whether this can ever happen in life is uncertain, but in living Bombus pennsylvanicus we were unable to bend, stretch, or compress the glossa in such a way as to cause evagination of the rod. It is clear that if the rod were evaginated the glossal canal would no longer exist and could not carry saliva.

At its distal end the glossal rod commonly expands to form the posterior surface of the flabellum. The expansion tapers basally toward its union with the rod, usually extending considerably farther basally than the base of flabellum, and is termed the bacular plate* (Figs. 8, 92E, 93B, 96C, 99D). If one tears the glossal rod from the glossa, the posterior surface of the flabellum often comes off with the rod.

An interesting parallel to the glossal rod is found in some colletids. Thus in Caupolicana, Colletes, etc., there is a rod-like or strip-like thickening in the anterior surface on each side, arising from the basiglossal sclerite, and extending lateroapically, supporting the sides of the broad, bilobed glossa.

In many bees there is a distal specialization* at the apex of the glossa. In the Colletidae this takes the form of the glossal lobes and brush. In many other short-tongued and a few long-tongued bees it is merely a small apical area, sometimes with the surface slightly differentiated, and bearing the distal seriate hairs; usually it lacks annuli. In these respects it resembles the glossal lobes of Colletidae, with which it is probably homologous. In a few short-tongued and most long-tongued bees, there is a constriction at the base of the distal specialization; the latter may be expanded and elaborately shaped. When such a constriction is present the area beyond it is termed the flabellum (labellum of some authors, e.g., Snodgrass, 1956, but not homologous to the labellum of Diptera). In the Ctenioschelini it is divided into a basal preflabellum* and a distal postflabellum* (Fig. 96E-G).

In addition to the annular and disannular hairs there are in many bees a few short and often blunt glossal setae (Figs. 52B, 60G, 93E, etc.), mostly near the apex of the glossa. They arise from distinct, commonly protuberant bases or sockets. It seems likely that they are chemoreceptors but in the absence of data on their functions, they are merely called setae. Fortunately there are no other types of setae on the glossa.

COMPARATIVE ACCOUNT

The paragraphs in this section are numbered, to facilitate cross referencing in other sections of this paper.

1. General form: 1.1 Major differences in the form of apoid glossae have been known for a long time (Reaumur, 1742) and have long been used in classifying bees (Kirby, 1802; Fabricius, 1804). Much of the diversity was illustrated by Saunders (1890) and by various other authors. Since the general form is well known for each group of bees, only a brief summary is included here.

1.2 In most bees the glossa ends in an acute apex (often modified, e.g., with a flabellum, and not acutely pointed when examined at higher magnifications). An acute apex is characteristic of all long-tongued bees (families Fideliidae, Megachilidae, Anthophoridae, and Apidae). (For an account of the mouthparts of these families see, Winston, 1979.) Most short-tongued bees (Andrenidae, Oxaeidae, Halictidae, Melittidae, Ctenoplectridae) also have an acute glossal apex and the glossa is strongly flattened, several to many times as broad as thick. The same shape is characteristic of males of the Australasian colletid genera Meroglossa and Palaeorhiza (Figs. 16, 19, 10, 21). Males of Amphylaeus, another Australian colletid genus, have a small median apical glossal projection (Fig. 12, 13) and are thus intermediate between the Meroglossa-Palaeorhiza condition and that of other colletids in which there is no sexual dimorphism in glossal form. Most Colletidae, i.e., all females and males of all genera except those mentioned above, have a broad glossa, the distal margin of which is gently convex, truncate, or usually bilobed (Figs. 1, 2, 14, 15, 18, 20). Because of the similarity of this shape to glossae of other Hymenoptera, the colletids have been widely regarded as the most primitive bees, but the truncate or bilobed glossa of colletids may be a reversion; see the Discussion section. The distal margin of the annulate surface is marked by the preapical fringe in most colletids; beyond this fringe are the glossal lobes which produce the broad and often emarginate glossal apex. Sometimes (Diphaglossa) the two glossal lobes are greatly extended so that the glossa is as long as in some long-tongued bees. The apex of the glossa in the Stenotritidae is rounded (Fig. 39).

1.3 The long-tongued bee families have a slender, somewhat flattened glossa, often less than twice as wide as thick (although occasionally much flattened, four or more times as wide as thick, as in Euglossini), usually parallel-sided in the basal region and tapering apically. The glossa is more slender and longer than in most short-tongued bees, but in spite of the terminology there are "short-tongued" bees with a glossa as long as in some long-tongued forms. The crucial difference between long- and short-tongued bees is not in the glossal length itself but in the labial palpi. In the long-tongued families the first two segments of these palpi are long, broad, sheath-like, and along with the galeae ensheath the glossa, forming a sucking apparatus with the protrusable and retractable glossa in the center. The third and fourth segments of the labial palpi are much shorter, usually more or less cylindrical and directed laterally. In the short-tongued families all four segments of the labial palpi are usually similar, cylindrical, and not sheath-like. Occasionally in some relatively long-tongued Panurginae (Andrenidae), the first segment of the labial palpus is much longer than the others and flattened; in the genus Melitturga the first two segments are long and flattened. Other differences between the long-tongued and short-tongued bee families are enumerated by Michener and Greenberg (1980). There is a general difference in glossal shape between short- and long-tongued bees that is partly independent of glossal length. In the former (except most colletids) the glossa is broad near the base, then narrows rapidly, but the apical part is usually drawn out, attenuate. In nearly all long-tongued bees the glossa narrows gradually toward the apex, but there is no particularly

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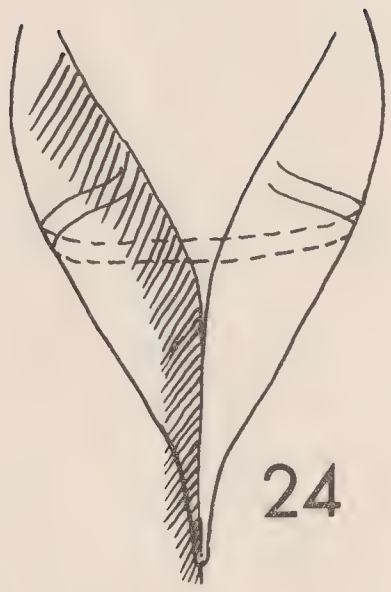

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attenuate apical region.

1.4 Long acute glossae probably arose from short acute glossae several times. Among "short-tongued bees" long glossae are found in such andrenid genera as Callonychium, Plesiopanurgus, Melitturga, and various species of other genera such as Perdita. Halictids like Thrinchostoma (especially the subgenus Diagonozus) and Rophites also have long glossae. Finally, the glossa is moderately long in the Ctenoplectridae, the sister group of the long-tongued bees proper (Michener and Greenberg, 1980).

2. Annulate surface: 2.1 The annulate surface is entirely or almost entirely anterior in Colletidae (except males of Meroglossa and Palaeorhiza) and Stenotritidae. At the sides of the glossa in these forms, annuli only curve part way toward the posterior surface and do not encroach on that surface (Figs 3, 40). In all other bees the annulate surface curves around the lateral parts of the glossa onto the posterior surface.

2.2 In the short-tongued bees this curvature results in the disannulate surface being narrowed, but at least largely exposed (Figs. 16, 17, 19, 22-30, 33-37, 39-46). In some preparations in the preapical part of the glossa, the lateral margins of the annulate surface meet or nearly meet along the posterior median line, virtually hiding the disannular surface in this region. This is especially so in dry material such as SEM preparations. For example in Fig. 51F, G (Calliopsis and Nomadopsis) a deep median groove is evident just basal to the flabellum. This is formed by the margins of the annulate surface drawing together. In a cleared preparation (Figs. 47, 48) the margins of the annulate surface are well apart, exposing the disannulate surface. In other species the seriate lines are seemingly fused for much of the length of the glossa so that the disannulate surface is limited to a basal and sometimes a small apical portion (Figs. 22, 31H, 32A). In certain Panurginae such as Psaenythia bergi, on the other hand, the margins of the annulate surface, at least in some preparations, curl into the glossa (except near the base and apex) so that the disannulate surface is depressed. In some preparations of Melitturga the lateral margins of the annulate surface in the middle part of the glossa approach one

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Figures 22-30. Diagrams of halictid glossae, posterior surfaces and cross-sections. 22, 23. Halictus quadricinctus. 24, 25. Corynura chilensis. 26, 27. Pseudaugochloropsis graminea. 28, 29. Nomia (Acunomia) melanderi. 30. Nomia (Epinomia) nevadensis. The pair of transverse lines across a glossa represent two annuli, the lines being broken where on anterior surface. Annular hairs and other annuli are omitted. For long glossae a median portion is omitted; the structures continued from basal to apical parts are joined by broken lines. For posterior views seriate hairs (or other disannular hairs) are shown only on the left, marginal hairs (when well developed) and setae (when present) are shown on the right. For sectional diagrams, annular surfaces are shown as solid lines, disannular as dotted lines or as a weak solid line (in other figures) if there is a glossal thickening. Disannular hairs are shown in sectional diagrams but annular hairs are omitted.

another so closely that there is a glossal groove, partly closed over by the lateral annular hairs; in this case the disannulate surface in this part of the glossa is invaginated as in long-tongued bees (Fig. 50).

2.3 In most long-tongued bees the annulate surface almost surrounds the glossa (Figs. 62-91). In many cases the margins of the annulate surface are deeply invaginated into the glossal groove which is therefore closed over by ordinary annular hairs, in addition to marginal hairs. This is true of Lithurge, Megachilinae, some Centridini (Epicharis), Anthophorini, some Exomalopsini (Tapinotaspis), Bombus, and others (Figs. 63, 65). In other cases, even within some of the same tribes or subfamilies, the lateral margins of the annulate surface are external, and the glossal groove is margined or closed over only by marginal hairs. This is the condition found in Fideliidae, Xylocopa, Nomadinae (Thalestria, Triepeolus), some Centridini (Centris), some Eucerini (Thygater), Melitomini (Melitoma), some Exomalopsini (Ancyloscelis), Apis, Euglossini, and Meliponinae. (The degree of invagination of the lateral margins of the annulate surface varies in different parts of the glossa, and in different preparations of the same species, so that it is not always a useful character.) In various parasitic long-tongued bees (Melectini, many Nomadinae, Nasutapis and Eucondylops in the Xylocopinae), the disannulate surface is not or scarcely invaginated, so that the lateral margins of the annulate surface are widely separated from one another as is usual in short-tongued bees (Figs. 79-81).

2.4 The annuli are generally moderately fine, numerous, and reasonably uniform. In most Colletidae, however, they are excessively fine and close together, either throughout or in a particular zone. Thus in genera such as Colletes, Scrapter, Euryglossa, Ptiloglossa, Hyleoides, and Leioproctus as well as females of Meroglossa, Palaeorhiza, and Amphylaeus, the annuli are fine and close, sometimes, as in Hyleoides (see McGinley, 1980), divided into distinctly different basal and apical zones. In contrast, Chilicola plebeia and males of Meroglossa, Palaeorhiza, and Amphylaeus, have moderately coarse annuli like those of other short-tongued bees. In Ptiloglossa and Diphaglossa the annuli are limited to a narrow zone basal to the preapical fringe. In contrast to most colletids, the annulation is especially coarse (i.e., annuli far apart) in the very long glossae of Euglossini (in the distal part of the glossa the distance between annuli may be over half the glossal width), in the reduced glossa of the parasitic allodapine Eucondylops, and in the Stenotritidae.

2.5 As noted in the section on Morphology and Terminology, the extremities of the annuli (= lateral margins of the annulate surface, along the marginal lines) vary among various groups. They may be abrupt or fade away. Often they are difficult to see, being hidden by the marginal hairs. Sometimes they reach the seriate lines so that the seriate and marginal lines are the same except near the base of the glossa. Sometimes in the middle part of the glossa the ends of the annuli closely approach the seriate hairs so that there is only a narrow zone between the seriate and marginal lines. In most bees, however, the annuli end far short of the seriate lines.

2.6 The annulate surface in Melectini as well as in Caenoprosopis in the Nomadinae appears to be minutely papillate (Figs. 96B, 98J).

3. Annular hairs: 3.1 In many bees the hairs arising from the annuli are slender, tapering from the bases to the sharply pointed apices. Deviations from that type are described below. There is a widespread tendency for the hairs to be broadened, usually medially or postmedially, although acutely pointed. This lanceolate shape, especially when only moderately broad, sometimes escapes notice on superficial examination because hairs are most easily examined along the sides of the glossa, where they are seen against a background light. Because the hairs there are seen on edge, their expansions are invisible. Lanceolate annular hairs occur at least near the apex of the glossa in some Dufoureinae (Fig. 38A-G) (but not other Halictidae), bees like Panurgus, Perdita, Protandrena bancrofti, Panurginus polytrichus, Callonychium flaviventre (but not other Andrenidae), and in most long-tongued bees. The hairs all appear to be tapering, not lanceolate, however, in Apis, Bombus, Melipona, Lestrimelitta, and some Trigona (in the Apidae) as well as in the parasitic allodapines Nasutapis and Eucondylops. In the Fideliidae and most Melectini and Ctenioschelini the hairs are also tapering except that some of the distal ones are slightly broadened (Figs. 60B; 96A-D). Most long-tongued bees have the lanceolate hairs limited to the distal part of the glossa, sometimes the area near the flabellum (e.g., in Exomalopsis solani which has only a few lanceolate hairs), and sometimes the distal fourth, half, or more. Variation often occurs even in related bees. Thus in Xenoglossa lanceolate hairs extend nearly to the base of the glossa while in Svastra they are limited to the distal part. The lanceolate hairs gradually grade into tapering hairs basally, so that as one looks along the glossa from base to apex it is impossible to say at what point they become lanceolate.

3.2 Many Nomadinae (Holcopasites, Nomada, Isepeolus, etc.) have broad, thin, imbricated scales forming a lamella along each side of the glossal groove (if present) or disannulate surface (Figs. 79, 80); frequently these lamellae overlap and hide the disannulate surface (or glossal groove if present) (Figs. 97G, I, K; 98A, E, I). These lamellae are often continuous, but sometimes seem to be made up of separate scales which may be modified marginal hairs; it is not clear whether or not they arise from the ends of the annuli. The apices of the scales can be simple and acute, blunt, or ending in two to several spines. Ancyloscelis in the Exomalopsini has similar lamellae (Fig. 92E). The Euglossini are unusual in that annular hairs are absent or greatly reduced on much of the anterior surface of the glossa, except near the base and apex. However, around the lateral margins of the glossa there are tapering hairs, becoming very large and lanceolate on the posterior parts of the annuli, sometimes with a slender hair before each annulus fades away toward the glossal groove. The large lanceolate hairs are directed somewhat mesally and cover over a channel formed by the gently concave posterior surface of the glossa (Figs. 86, 87).

3.3 Although males of the colletid genera Meroglossa and Palaeorhiza have tapering annular hairs, other colletids (including males of Amphylaeus) have glossal hairs which are minute, dense, short, flattened, truncated or emarginate, and usually capitate, with the apices commonly bent forward (Fig. 11). Such hairs are also found in

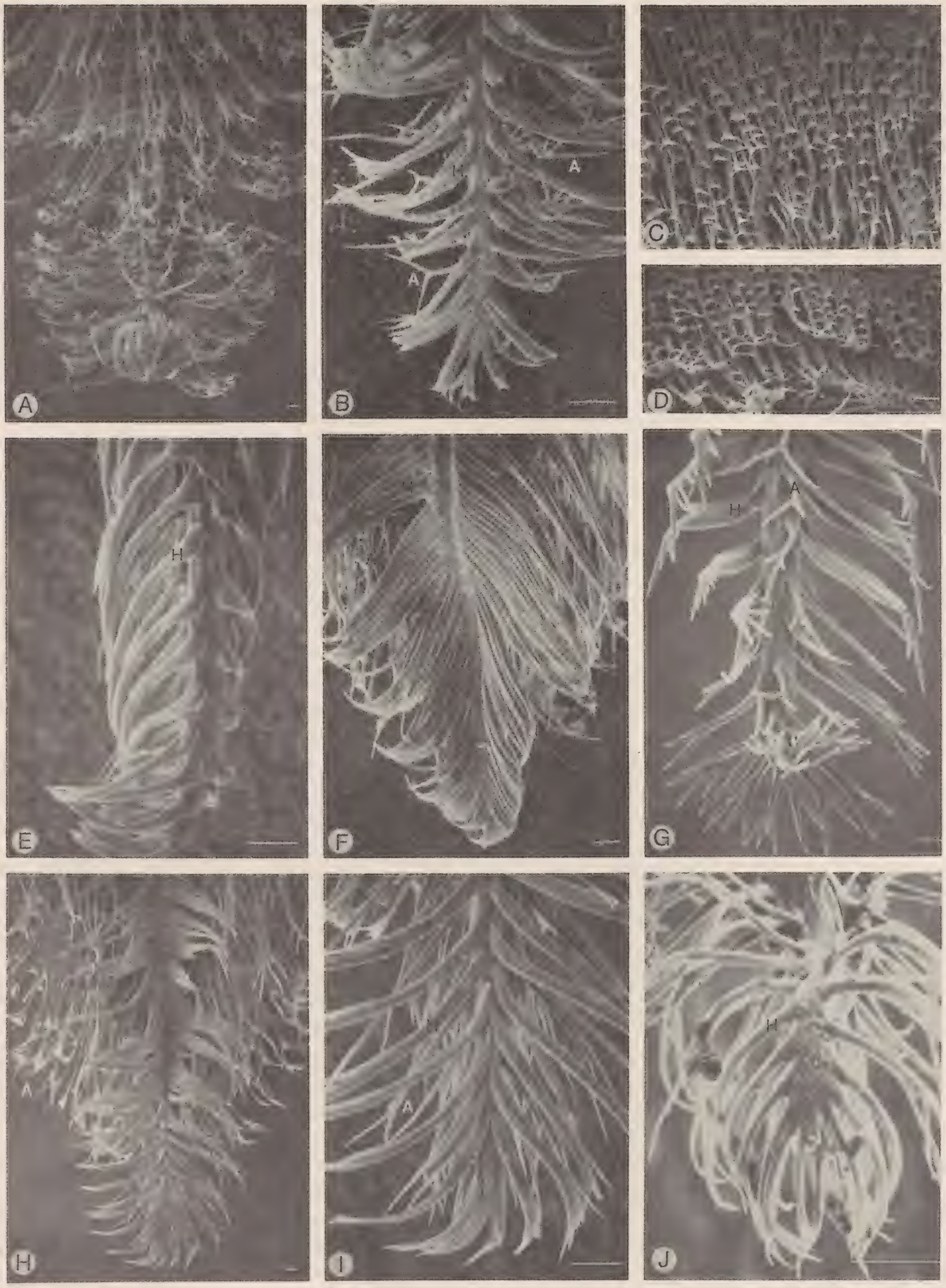

Figure 31. Apices of glossae and (C and D) annular hairs of Halictini and Nomioidini (Halictidae). Scale lines represent .01 mm;

the Stenotritidae, but not in other bees; similar hairs, however, are widespread in the Hymenoptera, from Tenthredinidae (Tenthredo) and Ichneumonidae (Cryptus) to sphecoid wasps such as Sphex, Philanthus, and Oxybelus. Such hairs may therefore be plesiomorphic.

3.4 The remaining group of bees which commonly has annular hairs that deviate from the simple, tapering type is the Halictidae. The simple, tapering type is found in the Dufoureinae, with lanceolate hairs preapically in some (Fig. 33E, G). In Dufourea, however, at least some of the hairs in the middle part of the glossa are divergently bifid preapically. In Nomia (Nomiinae) at least some hairs on the preapical part of the glossa are divergently bifid preapically (Fig. 32H). In Halictinae most of the annular hairs are preapically bifid, or they are expanded preapically with two divergent prongs and often one to several points between (Figs. 31A, C, D, H, I; 32A, E).

4. Disannulate surface: 4.1 This is the converse of the annulate surface. In bees in which the annulate surface does not wrap around the glossa, the disannulate surface is fully exposed, while in those whose annulate surface wraps around, the disannulate surface is exposed only at the base and apex. In short-tongued bees the disannulate surface is usually broadly exposed. Commonly it is gently concave (strongly so in some forms like Rophites, Melitturga, and sometimes in Dufourea and Nomia) forming a longitudinal depression at least in the basal part of the glossa. In the distal part of the glossa, where it is attenuate, the disannulate surface usually occupies the entire posterior surface.

4.2 In most long-tongued bees, except for its extreme base and apex, the disannulate surface is invaginated and forms the glossal canal (Figs. 9, 63, etc.). The surface seems to be incompletely invaginated in Fideliidae (Fig. 62) and Tapinotaspis (Fig. 68) but this may be an artifact of preparation. In many common long-tongued bees the canal and glossal rod can be evaginated in the middle part of the glossa, as noted earlier and illustrated in sectional diagrams (Figs. 65, 69, 72, 75, 83, 85, 91). In the parasitic allodapine Nasutapis, the invagination is incomplete, the glossal groove being quite wide in the basal part of the glossa, and in Eucondylops there is no invagination, the disannular surface being a mere flat membrane as in many short-tongued bees. The same is true of Nomada and some other Nomadinae as well as Melectini (Figs. 73, 78-81), although the glossa is quite elongate.

4.3 In short-tongued bees the disannulate surface is unsclerotized, transparent in cleared specimens. However, in certain species the zone between the seriate lines, i.e., the glossal thickening, is somewhat tougher than the cuticle lateral to it and can be torn out more or less intact from the posterior surface of the glossa in specimens prepared in KOH. The seriate hairs remain attached to such a fragment, at least on one margin. Bees having such a recognizable glossal thickening include Perdita (at least P. acapulcona), Panurgus,

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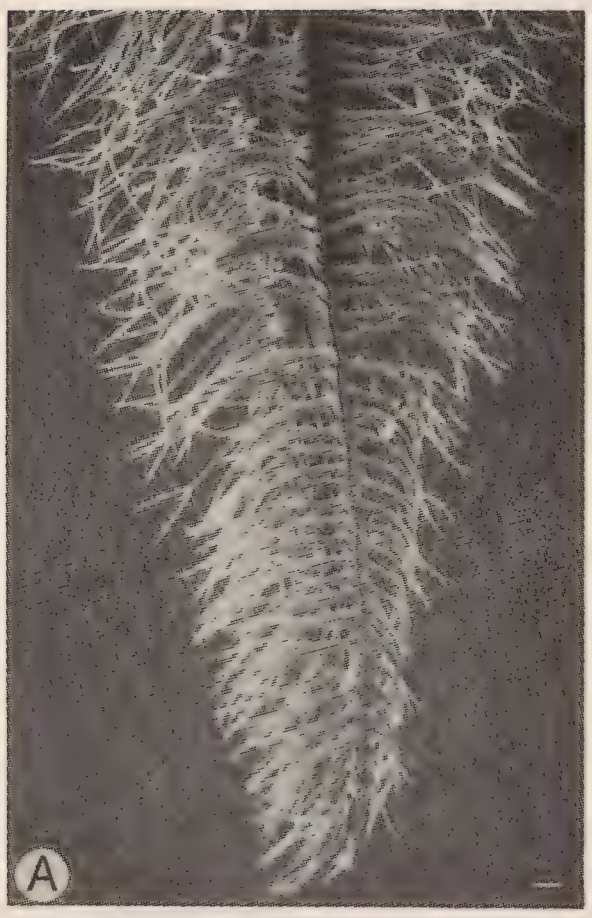
H = seriate hair, A = annular hair. A, Lasioglossum (Hemihalictus) lustrans, anterior view. B, Lasioglossum (Sphecodogastra) texanum, posterior view. C, Same species. D, Sphecodes gibbus. E, Halictus ligatus, posterolateral view. F, Sphecodes gibbus, posterior view. G, Thrinchostoma productum, anterior view. H, I, Pseudagapostemon divaricatus, posterior views. J, Nomioides divisa, posterior view.

Rophites, and Systropha. In Rophites the structure looks much like a true glossal rod (see below). Other forms, such as Andrena and Melitturga, have a weak glossal thickening which is narrow and not associated with seriate hairs. Calliopsis and some allied panurgines have distinct glossal thickenings but no seriate hairs. (Glossal thickenings of short-tongued bees, when present, are shown as solid rather than dotted lines in the sectional diagrams.) Some andrenids, halictids, and melittids have the seriate lines approximate or fused distally or for most of the length of the glossa (Fig. 31H), bearing long and commonly branched seriate hairs with broad, flattened bases on at least the united part of the seriate lines (Figs. 31E, I; 32B, G). In such cases the united or approximate seriate lines are also somewhat tough and can be torn out from the posterior integument of the glossa.

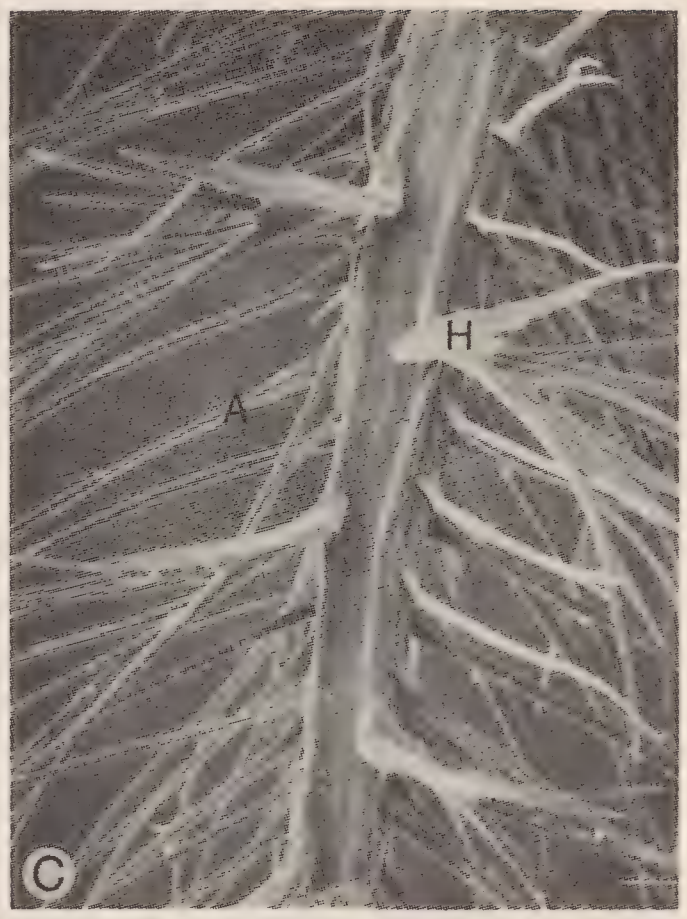
4.4 A glossal thickening such as is found in Panurgus is shallowly trough-shaped, with the seriate hairs along the lateral margins (Fig. 51D). This is similar to the glossal rod of many long-tongued bees except that the latter is sclerotized, much more slender, and extends for the full length of the glossa. The fideliids (at least Neofidelia) have such a glossal rod, not or scarcely invaginated into the glossal groove in our preparations, with the entire space between the seriate lines sclerotized and part of the rod (Fig. 62). The same (but with deep invagination) is true of Lithurge, Ancyloscelis, the Eucerini, Anthophorini, Centris, etc., except that in most of these the amount of sclerotization (darkening) is less, so that there is a median rod occupying the bottom of the trough, lateral to which are the unsclerotized seriate lines (ridges). Tapinotaspis is similar but with these ridges quite high (Fig. 68); they are still higher and partially enclose a distinct bacular canal in Epicharis and especially in Xylocopa, Melipona, and Apis (Figs. 77, 82, 88, 89). In many Megachilinae the sclerotized rod is limited to the bottom of the trough, with the hair-bearing summits of the seriate lines (ridges) being also but less strongly sclerotized, so that there seem to be three rods, the median one stronger than the others (Fig. 65).

4.5 In the Apidae the rod tends to look double because of thickening on each side of the mid line (Figs. 86-91). In Bombus and Euplusia the median strip is pale, with a dark band on either side; in Euglossa there is a weak median thickening in addition to lateral ones. In the Meliponinae and Apinae the seriate ridges nearly close over the bacular canal, which is further enclosed by the inward-directed, minute seriate hairs. In the same taxa as well as Xylocopa the seriate ridges are sclerotized or at least prismatic, and become part of the rod, which therefore nearly encloses the bacular canal.

Figure 32. Apices (and preapical part, C) of glossae of Augochlorini and Nomiinae (Halictidae). Symbols as for Figure 31. A, B, Paroxystoglossa transversa, posterior view, three preapical serial hairs broken off. C, Pseudaugochloropsis graminea, posterior view of preapical part. D, Same species, posterolateral view. E, Augochloropsis metallica, anterior view. F, Same, posterior view, a seriate hair broken off. G, Nomia nevadensis, posterolateral view. H, I, Nomia nortoni, anterior and posterior views.


A


H
A
B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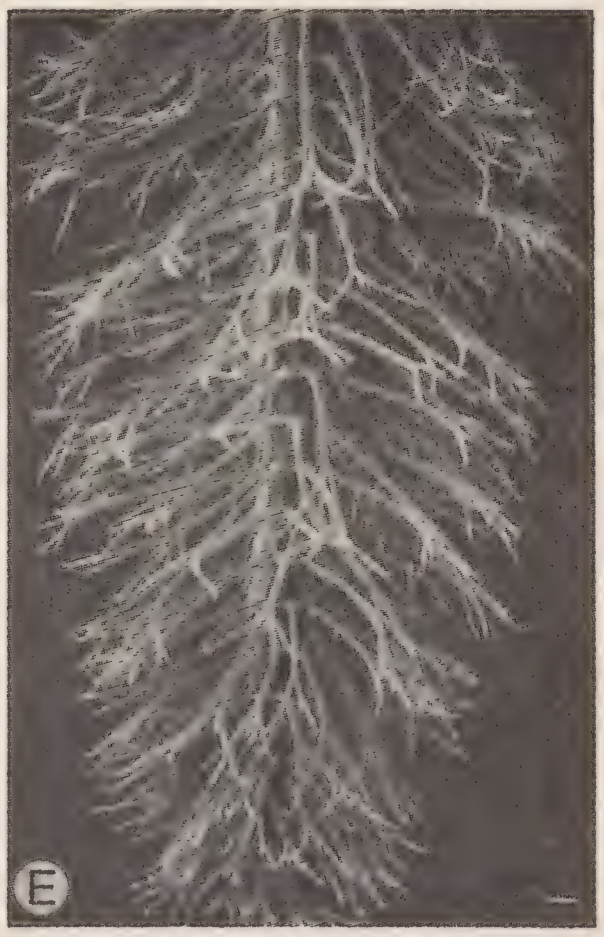
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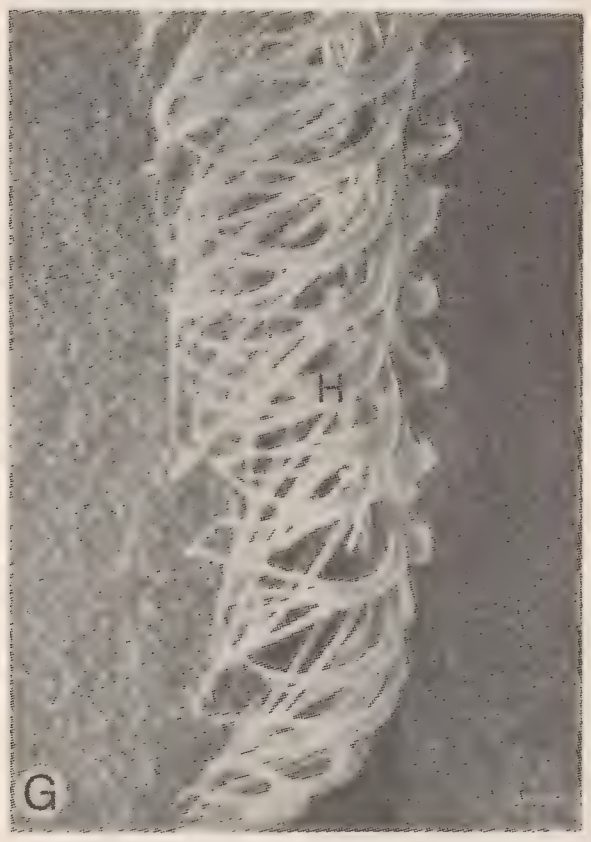
H
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H


H
I

4.6 Finally, there are a few long-tongued bees, all parasitic Anthophoridae, that have lost the rod or retain at most a feeble glossal thickening. These are Eucondylops, Nasutapis, and various Nomadinae such as Nomada and Biastes, and Melectini such as Xeromelecta.

5. Disannulate hairs: (This section does not describe the disannulate hairs on flabella or flabellum-like apical areas.) 5.1 In some bees the disannulate surface is hairy. For example, in Stenotritidae (Fig. 39) it is covered with long hairs, longer than the annular hairs, except for a bare basal triangular area. In Colletidae there are many intermediates from hairy to bare (Figs. 2, 13, 15, 20), except that the glossal lobes always bear long hairs forming the glossal brush. Thus in Amphylaeus the surface is densely hairy, with a weak longitudinal band of denser hair in the male; denser hairs that might be called marginal hairs are present lateroapically. In Chilicola the surface is also largely hairy with a slender, triangular, longitudinal median, bare area, widest at the base of the glossa; midapically the hairs grade into large, branched hairs like those of the glossal brush. In Euryglossa the surface is covered with short, rather sparse hairs, sparsest before the glossal brush. In most other colletids examined the surface is half half to largely bare, often with small hairs on the basal third of the glossa and extending apically as a broad median zone, but with a longitudinal median bare strip (for example in the female of Meroglossa), widened basally, or with a basal bare triangle, sometimes depressed (e.g., in Colletes).

5.2 The lateral margins of the bare median triangle or strip found in various colletids may represent the seriate lines of other families. No such lines are present in stenotritids. The seriate lines of other short-tongued bees are widely separated basally but converge toward the apex of the glossa; sometimes they meet forming a basal triangular area suggesting that often seen in colletids. Just before the apex, the seriate lines often diverge, spreading to the lateral margins of any flabellum-like structure that may be present.

5.3 In Eucondylops (a parasitic allodapine anthophorid whose glossa suggests that of a short-tongued bee) there seem to be no seriate lines or hairs and the disannular surface is bare. The same is true of some andrenids such as Calliopsis (Fig. 47).

5.4 In melittids, oxaeids (Fig. 41), Nomia nevadensis, and some andrenids, the seriate lines appear to be absent except on the distal part of the glossa, where they bear enlarged seriate hairs. In some such cases, the seriate lines may be fused with the marginal lines, as is shown for example in Macropis by the basal separation of these lines, leaving a bare laterobasal area between the two (Fig. 55). Even in Melitturga, in which the disannulate surface of the long glossa is strongly invaginated and largely hidden in the glossal groove, no seriate lines are recognizable, perhaps because they are united with the marginal lines (Fig. 49).

5.5 In many other panurgines (Panurgus, Heterosarus, Perdita, Psaenythia, Metapsaenythia, Pterosarus, Protandrena, Pseudopanurgus) (Fig. 45), and in Dufourea (Fig. 33), Ctenoplectra (Fig. 57), and others, the seriate lines are recognizable and separate from the marginal lines for much of the length of the glossa, each frequently bearing a row or narrow band of hairs. In Macropis these lines are

easily recognizable for their full lengths, even where they are united with the marginal lines, by the series of long hairs on them (Fig. 55).

5.6 In Nomia melanderi the seriate lines are distinct for almost the full length of the glossa (Fig. 28), but hairless except for the large hairs at the glossal apex. The male of Meroglossa is similar but for their full lengths the seriate lines give rise to large, branched hairs (Fig. 16). In the Halictinae as well as in most Dufoureinae, the seriate lines are likewise distinct, and each bears a continuous fringe of long, usually simple hairs which grade, in Halictinae, into long, branched, seriate hairs near the glossal apex. An exception to this statement is found in Thrinchostoma in which there is a gap between simple seriate hairs near the glossal base and branched ones apically.

5.7 In the Halictinae, in Melittidae (except Dasypoda and Macropis), and in Nomia nevadensis, Heterosarus (some preparations), Psaenythia, and Metapsaenythia the seriate lines come very close together in the distal, attenuate part of the glossa and commonly fuse indistinguishably, sometimes to the extent that the bases of the large, branched, seriate hairs form a single row with alternate hairs directed toward opposite sides. Such fusion or near fusion is often limited to the apical half or much less of the glossa. However, in Halictus (Fig. 22), Lasioglossum (s.l.), Homalictus, and Agapostemon the seriate lines are approximate except for the basal sixth to tenth of the glossa where they diverge toward the glossal base. The same is true of Augochlora, Pseudaugochloropsis (Fig. 26), Megalopta, Paroxystoglossa (Fig. 32A), etc.; moreover, in these genera the large, branched, seriate hairs like those of the glossal apex extend nearly to its base.

5.8 When the seriate lines are close together, especially near the apex of the glossa, the interval between them is commonly represented by a groove, which usually terminates abruptly at about the base of any distal glossal specialization. This groove is shown in many of the SEM illustrations of glossal apices (e.g., Figs. 38D, F; 51F, J, etc.).

5.9 In the genus Perdita the seriate lines form strong, rounded ridges running the length of the glossa. These ridges are divided into short segments by numerous transverse grooves (Figs. 52B, C), so that they sometimes appear as a series of scales (hair bases?), and in most species examined (not P. texana) each segment is drawn out laterally into a point or short hair. In P. texana the basal parts of the seriate ridges are not divided by grooves and bear numerous short seriate hairs. In the same species, robust, pointed setae are scattered along the lateral parts of the seriate ridges in the distal part of the glossa, where these setae are larger and more conspicuous than the annular hairs which are restricted to the anterior surface. In P. acapulcona, also, there appear to be large setae occupying the positions of marginal hairs near the apex of the glossa, but no such setae are visible in the SEM photographs of smaller species; a few, short, probable setae are in this position in P. albipennis.

5.10 In long-tongued bees the seriate hairs, when present, are minute, simple, and directed distomesally. (In short-tongued bees they are directed laterally or distolaterally.) They are absent, as are the seriate lines, in Eucondylops, and the hairs are absent or nearly so in various Nomadinae such as Holcopasites, Caenoprosopis, Biastes, Nomada, and Isepeolus. They are present in Triepeolus and Thalestria, although

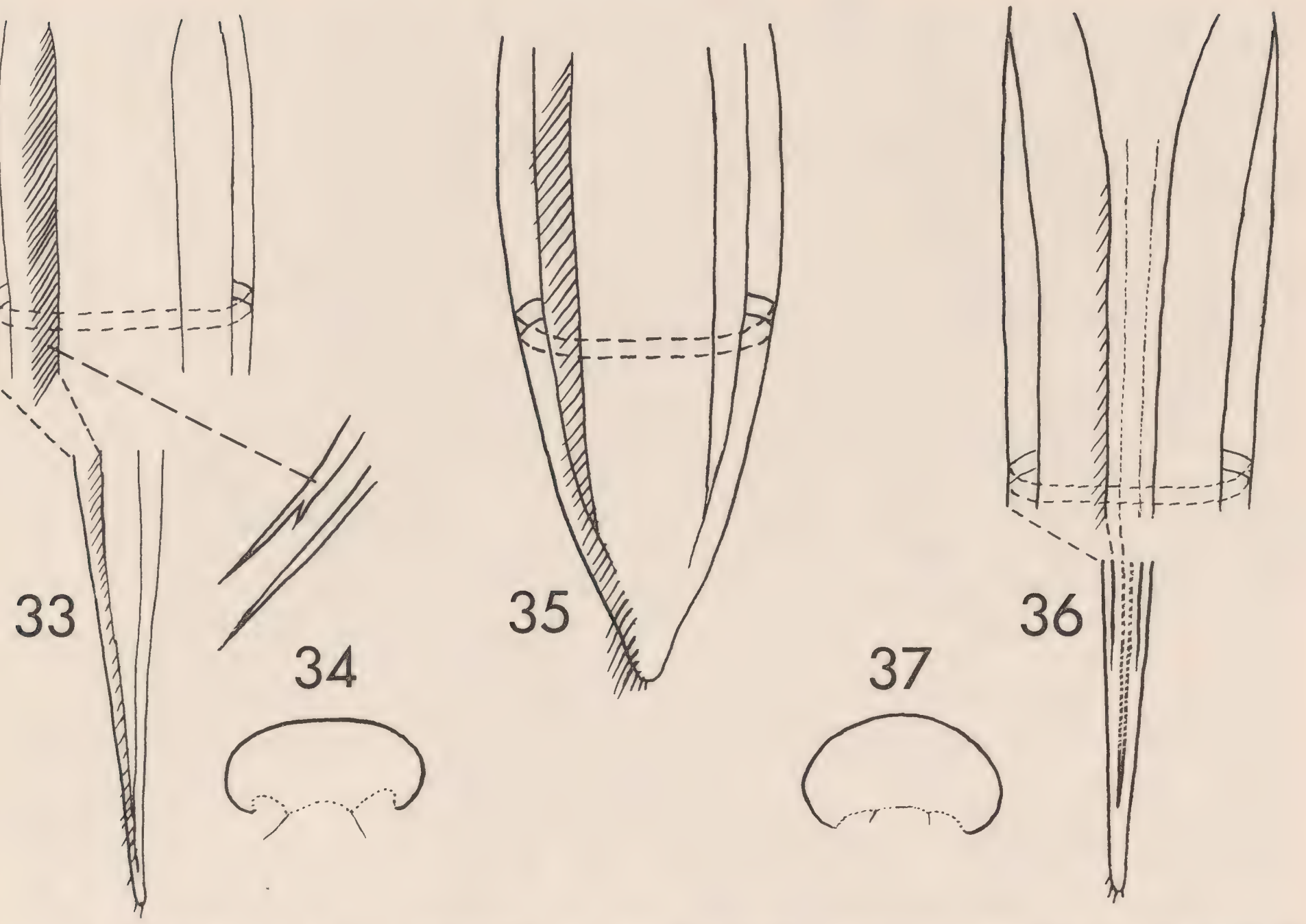
absent from the distal part of the glossa in the former. Sometimes, as in Centris, the seriate hairs seem to be fused into a longitudinal sheet, sometimes broken (naturally or in preparation?) into separate hairs. The same is true to greater or lesser degrees in various other Anthophoridae. In Anthophora and Amegilla the seriate hairs are large for long-tongued bees, and each arises from a laterally expanded hair base suggesting similar hair bases in Perdita. In Perdita each scale-like hair base gives rise to an extremely short, laterally directed hair while in the Anthophorini each gives rise to a much larger, mesally directed hair.

5.11 Although in short-tongued bees other than colletids and stenotritids it is rare to find hairs on the disannulate surface other than the seriate hairs and some marginal hairs, in long-tongued bees minute hairs in the space between the marginal and seriate lines are present in Xylocopa, Triepeolus, Centris, Anthophorini, Eucerini, Exomalopsini, Bombinae, some Meliponinae, and Apinae. These hairs project into the glossal canal but are usually rather sparse and trivial in length compared to the diameter of the canal. Even when present, such hairs may not be found all along the glossa. Thus they do not appear in some sectional diagrams (Figs. 62-81) of species that possess them.

6. Distal specialization (nonflabellate): 6.1 In a rather small number of bees there is no striking distal specialization. As in most sphecoid wasps, the annulate and disannulate surfaces meet at the apex with no special features. This is approximately the situation in Stenotritidae (Fig. 39), in which the apex of the short glossa is rounded, with some rather long hairs, a continuation of those of the disannulate surface, a few of them deeply forked. The parasitic anthophorid bees Nasutapis (Fig. 100I) and Eucondylops have slender, pointed glossae, without any indications of specialized apical areas or of special types of hairs in that region. The panurgine genus Panurgus also shows no appreciable distal specialization (Figs. 51D, E). The same is true for Perdita texana (but not of other species of Perdita examined), except that it has at least one blunt seta arising near the glossal apex, in addition to tapering setae scattered along the distal part of the glossa on the posterior surface.

6.2 Most bees have some sort of apical glossal structure, or at least hairs noticeably different from those of more proximal parts of the glossa. This statement is debatable for the groups discussed below in paragraph 6.4 and the first part of 6.5; in these forms the distal specialization is not defined but involves only progressive changes in the hairs and forward curvature of the slender glossal apex. In Colletidae (except males of Meroglossa and Palaeorhiza) the distal specialization consists of the glossal lobes (Fig. 1) which form the broad and commonly bilobed apex of the glossa. An exception is in male Amphylaeus, in which there is only one rather narrow, median apical lobe (Figs. 12, 13). The glossal lobes bear on both anterior and posterior surfaces disannular hairs forming the glossal brush. These hairs are commonly branched but are merely bifid (some of them simple) in female Meroglossa and appear simple in Euryglossinae.

6.3 In Colletes, Hylaeus, and male Amphylaeus (but not in other colletids) the hairs of the glossal brush are arranged to form weak an-



Figures 33-37. Diagrams of dufoureine glossae, posterior surfaces and cross-sections (Halictidae). 33, 34. Dufourea marginata. 35. Micralictoides altadenae. 36, 37. Systropha curvicornis. Explanation as for Figures 22-30.

nuli, each broken into short sections in Hylaeus. Annuli on the glossal lobes could indicate that we are incorrect in attributing these lobes to the disannular surface. However, they are distinctly different from annuli on the annulate surface and the hairs are similar to those on the seriate lines of many other short-tongued bees. We believe that the annuli on the lobes are secondary features, not homologous to the normal annuli. This possibility is supported by the observation that hairs are arranged in transverse rows (annuli) on the paraglossae of some bees (e.g., Meganomia); thus transverse rows of hairs and therefore annuli could arise independently on different areas.

6.4 In most of the remaining short-tongued bees the apex of the glossa is pointed, often curved anteriorly, usually attenuate, slightly convex posteriorly, with annuli recognizable nearly to the apex on the anterior surface but absent from the posterior surface, which is largely occupied by the distal parts of the seriate lines, often unrecognizably fused. The hairs on the posterior surface are therefore the distal seriate hairs. As noted previously, there is often a groove (representing the space between the seriate lines) that ends basal to or within the most slender, terminal part of the glossa. The seriate hairs, diverging laterally and usually curving apicad and branched, are large, usually robust and flattened at their bases. When the seriate

lines are united, and when the hair bases are large, the hairs almost form a single row, those extending to one side alternating with those extending toward the other.

6.5 Glossal apices of the general type described in 6.4 are found in males of Meroglossa and Palaeorhiza (but distal seriate hairs not as large as those nearer the glossal base), all Halictinae, Nomiinae, Melittidae, Oxaeidae, Andreninae, and the following genera of Panurginae: Xenopanurgus, Heterosarus, Metapsaenythia, Pterosarus, Protandrena, Cephalurgus, Liphanthus, and Epimethia. In some other panurgines, however, such as Panurginus, Psaenythia, Protandrena bancrofti (slightly, Fig. 51B), Pseudopanurgus aethiops (slightly, Fig. 45), and P. herbsti, the seriate lines and hair rows diverge markedly preapically, partially enclosing a convex apical area on the posterior side of the glossa suggestive of a flabellum. The same is true of the halictid, Nomioides (Fig. 31J). The glossa as a whole is not constricted at the base of this area; hence we do not call such an area a flabellum. However, the disannulate surface may be narrow or a mere groove, which does widen to form the apical area on the posterior surface of the glossa, enhancing the flabellum-like aspect. In Panurginus and perhaps some others listed above, specimens cleared in KOH show the disannulate surface moderately broad preapically, not narrowed basal to the apical area, while SEM shows the seriate lines approximate preapically, diverging to enclose the apical area. Dasypoda has a gradual distal glossal broadening, with a broad "cobblestoned" posterior surface (Fig. 59A, B), which we arbitrarily do not call a flabellum because of its length and the numerous annuli on its anterior surface.

6.6 Certain other panurgine bees such as Nomadopsis scutellaris and Hypomacrotera are similar but the posterior, bare, convex, apical area is broader, the seriate hairs being extensions of the margins of the area. These hairs are part of the same series as the other seriate hairs when the latter are present. Although some are branched, at least at the extreme apex of the glossa, they are smaller than the large seriate hairs of halictids and others. Spinoliella and Arhysosage are similar but the marginal hairs of the apical area are reduced to mere small, unbranched, thorns.

6.7 Dufourea, Rophites, and Systropha also have a flat or convex apical area on the posterior surface of the glossa, this region being not or only slightly wider than the glossa basal to it. It is formed by termination of the groove between the seriate lines and reduction in the size of all the apical hairs of the glossa so that hair bases do not interrupt the flat or convex surface (Figs. 38A-G). The seriate hairs are small and arise from the margins and apex of the apical area, or in Rophites they are absent or nearly so; these hairs are branched in Dufourea, simple in Systropha. Possibly some of the simple hairs on the anterior surface of the glossal apex are seriate hairs but probably they are annulate hairs, differing from those of the preapical part of the glossa by being slender and simple.

6.8 The panurgine genera Camptopoeum and Plesiopanurgus have a similar glossal apex, with reduced lateral hairs, which are, however, perhaps setae. The apical area is broadly connected to the space between the seriate lines, which is thus broad for the whole length of

the glossa. The seriate hairs are small and simple.

6.9 Some long-tongued bees also lack flabella. In the nomadine genera Epeolus, Triepeolus, and Isepeolus the extreme apex of the glossa is simply irregular and bare, with a few setae projecting apically from both upper and lower surfaces (Fig. 97A, F). Doeringiella and especially Thalestria are similar, but with the area flattened with a distinct edge and thus more like a flabellum (Fig. 97B, E); Epeolus approaches Doeringiella in this feature.

6.10 In the anthophorine genera Habropoda and Emphoropsis there is no flabellum (Fig. 95E, F). The annulate part of the glossa abruptly narrows; annular hairs which are broadly lanceolate or truncate arise to its very apex on the anterior surface. The posterior surface of the abruptly narrowing part of the glossa, which is beyond the apex of the glossal groove, is flat and bare. Setae have not been recognized in this region, but the broad annular hairs cover so much of the surface that SEM photographs might not show them. Setae are, however, scattered among the annuli on the posterolateral parts of the glossa (considerably lateral to the groove) from near the apex of the groove to the middle of the glossa in Emphoropsis at least.

7. Flabellum: 7.1 The flabellum is a type of distal specialization recognized by its basal constriction, separating it from the rest of the glossa. All intergradations exist between flabellate and non-flabellate glossae, and sometimes one must make an arbitrary decision as to whether to call a given distal specialization a flabellum or not. The posterior surface of the flabellum is convex, hairless (hairs, setae, or processes sometimes present along distal and lateral margins), and its margins converge basally to connect with the rest of the seriate lines, so that the posterior flabellar surface is continuous with the cuticle between the seriate lines. In long-tongued bees this means that the posterior flabellar cuticle connects with the glossal rod; if one tears out the glossal rod, the posterior but not the anterior surface of the flabellum often comes out attached to the rod. From this finding, and from the observation that the hairs of the concave anterior surface of the flabellum are disannular hairs, similar to those of the disannulate surface of the rest of the glossa, it appears that the flabellum (or only part of it in Meliturgula and Ctenoplectra) is an elaboration of the disannulate surface. It is thus comparable to the glossal lobes of Colletidae. Annuli are absent on the flabellum, with the exception of a few forms such as Thalestria, Meliturgula, and Ctenoplectra. In Thalestria the flabellum-like, posterior, bare, glossal area is similar to that of its close epeoline relatives, but is elongated apparently by the basad extension of the bare area. This results in annuli being on what appears to be the anterior surface of the "flabellum." In a few other bees without or with only a weakly defined flabellum, the same thing may have occurred. This may include Meliturgula and Ctenoplectra, which have annuli on the anterior surface of an elongate flabellum.

7.2 Some panurgine genera are similar to Panurginus, Pseudopanurgus, etc., but with the apical, bare area clearly broader than the glossa at the base of that area, and thus forming, by definition, a flabellum margined by long processes. These processes or hairs, however, are simple and tapering, sometimes united in pairs (or threes)

at their bases, so that they could be interpreted as branched. The concave, anterior side of the flabellum has numerous small, simple, disannular hairs. Examples of such glossae (Fig. 47; 51F-J) are found in Liopoeum trifasciatum, Nomadopsis zebrata, and Calliopsis. In Liopoeum hirsutulum the marginal processes are very short and rather sparse.

7.3 In Callonychium the flabellum is short, broader than long, with only minute, short, marginal processes. However, a series of setae arises from the concavity on the anterior surface of the flabellum, among a few much smaller, disannular hairs. The row of well spaced setae continues basally on the posterior surface, lateral to the narrowing base of the bare, posterior, flabellar surface (Fig. 52D, E). Perdita, except for P. texana which lacks a flabellum, is similar to Callonychium but the margins of the flabellum are simple (Fig. 52A-C).

7.4 Melitturga has a peculiar flabellum with a narrow base, short hairs on the anterior surface and thick, blunt hairs (or tapering pegs) on the posterior surface, some of the largest, lateral pegs being bifid (Fig. 49). These structures are not setae; perhaps they are modified disannular hairs.

7.5 Another unusual glossal apex is that of the panurgine Meliturgula. It is only slightly broadened, thus doubtfully a flabellum, and is elongate with five or six annuli recognizable on its anterior surface. There are no disannular hairs on the distal area and its margins are lobed as in some species of Ctenoplectra.

7.6 The Ctenoplectridae (Ctenoplectra) have a flabellum shaped like that of Meliturgula, with annuli on the anterior surface, and with lobed margins, the lobes sometimes acute and possibly derived from disannular hairs (Fig. 59F, I). On the concave anterior side of the glossal apex, near the margins, there are several distinct setae.

7.7 In many long-tongued bees the flabellum is of a type here called placoid, i.e., it is smooth and convex on the posterior surface, with the distal and lateral margins entire (Fig. 92). The lateral margins continue as converging lines on the posterior surface of the glossa and appear to be continuous with the seriate lines along the glossal rod. The anterior surface bears a few to numerous small, disannular hairs, usually so short as to be invisible in posterior view. Similar small hairs are often continued around the sides of the base of the flabellum and are continuous with the disannular hairs of the main part of the glossa. A series of setae (sometimes only two or four) crosses the glossa just basal to the flabellum on the anterior surface and sometimes extends along each side onto the posterior glossal surface and basally for a short distance lateral to the distal end of the glossal groove. These setae are often long enough that their apices radiate conspicuously beyond the flabellum as seen in posterior view (Fig. 98I). Placoid flabella occur in all Fideliidae, Megachilidae, Exomalopsini, Melitomini, and in the allodapine genera Allodape and Braunsapis (Ceratinini). The panurgine genera Perdita (except texana) and Callonychium have similar flabella (the glossal groove is absent).

7.8 A minor modification of the placoid type of flabellum occurs with reduction of the distal part of the flabellum (or perhaps it is distad migration of the transverse row of setae). The flabellum looks typically placoid as seen from the posterior side, including the presence of a few setae radiating beyond the flagellar margin. From the

anterior side, however, it can be seen that the flabellum extends only a short distance beyond the setal bases, so that the small, simple, disannular hairs arising from the anterior surface of the flabellum beyond the setae are restricted to a narrow preapical zone. (Sometimes, as in Nomada, some of these hairs, as well as the setae, extend beyond the flabellar apex.) Such flabella are found in Nomada (Nomadini) (Fig. 98C) and, Manuelia (Fig. 99F) (Ceratinini) and others. Macrogalea (Fig. 99J) is similar but the rather elongate flabellum lacks the small disannular hairs on its anterior surface.

7.9 A further step in the same direction, in which the disannular hairs on the anterior surface of the flabellum are absent or nearly so and the setae arise just beneath the apex of the flabellum, occurs in the following Nomadinae: Caenoprosopis, Holcopasites (Fig. 98F), Morgania (Fig. 98D), Biastes, Ammobatoides, Neolarra (Fig. 98K, L) (bases of two of the lateral setae cause indentations in the converging basolateral margins of the posterior surface of the flabellum), Epeoloides (Fig. 97L), and Leiopodus (Fig. 97H).

7.10 Pseudodichroa is similar to the "pasitine" bees listed in the above paragraph except that a few setae appear to have moved mesad onto the basal part of the posterior surface of the flabellum, so that the main part of the flabellum is surrounded by a ring of setae (Fig. 98H). Osiris has the setae rather scattered instead of in a neat row, on the apical part of a thickened flabellum that lacks a thin apical edge and has some transverse apical wrinkles (Fig. 97I, J, M).

7.11 Certain other Nomadinae (Epeolus, Triepeolus, Doeringiella, and Isepeolus) do not have a flabellum but their distal specialization is apparently a result of further flabellar reduction and migration of some of the setae onto its posterior surface (Fig. 97A-F). Thalestria is similar but a bare, flabellum-like area extends basad on the posterior surface; on the corresponding anterior surface there are numerous annuli and annular hairs.

7.12 A modification of the placoid type of flabellum is found in the Bombini, Meliponinae, and Apinae (Apis) (Figs. 100F-H; 101). In these forms the flabellum is rather short and broad, its lateral margins converge strongly basad, together forming a convex or nearly transverse base; apically the flabellum extends far beyond the setae which form a row across its base on the anterior surface; only in some Trigona do the setae extend beyond the lateral (not distal) margins of the flabellum. The small, anterior, disannular hairs of the flabellum are numerous and some of them arise at the flabellar margin and extend beyond it; these hairs are mostly simple but the marginal ones are branched in Apis. Basally the small hairs continue in a usually dense mass across the preflabellar area of the posterior side of the glossa, especially in Bombini (Fig. 100F) and Apis. The flabellar margin is irregularly shallowly lobed rather than entire in Bombus, Lestrimelitta, and Apis.

7.13 Canephorula (Canephorulini) has a rather elongate flabellum, the posterior surface smooth, the apex irregularly lobed (Fig. 94G-I). Its remarkable feature is the anterior surface, on which the numerous small disannular hairs are slender at the flabellar base but have large bases with short, attenuate apices medially and distally, along the lateral margins becoming coarse and peg-like; some such hairs project as flattened pegs beyond the apical flabellar margin. A few setae are

present sublaterally, mixed with small hairs, to a point beyond the middle of the flabellum rather than across its base.

7.14 Coarsely pebbled or cobblestone-like posterior surfaces of flabella characterize the Eucerini (Fig. 94A-F). Otherwise they are placoid (unusually elongate in Thygater). The small disannular hairs on the anterior side are numerous, at least the distal ones mostly branched, some arising from the very apex of the flabellum as in Apis. As in Canephorula, setae arise among the small hairs of the anterior surface, sublaterally, usually to a point beyond the middle of the flabellum; there are no setae across the base of the flabellum as described above for placoid flabella. Similarly cobblestone-like posterior surfaces characterize flabella of the Centridini (Fig. 96H-J). However, in this tribe the flabellum is elongate, the small hairs on the anterior surface are simple and reduced toward the apex, and setae are present near the base, but not on the flabellum. The same remarks apply to Deltoptila (Anthophorini) (Fig. 95D, G), in which the distal and lateral small hairs of the anterior surface are blunt and capitate.

7.15 Cobblestone-like posterior flabellar surfaces also occur in Melectini (Fig. 96A-D), especially in Melecta, but in Thyreus the "stones" are in transverse rows and in Xeromelecta the surface is only irregularly transversely wrinkled. As in Nomada, Manuelia, etc., the distal part of the flabellum appears to be reduced so that the setae arise on its anterior surface near the apex; they do not, however, radiate beyond the flabellar margin except laterally, but they are arranged across the anterior surface preapically and around the sides to the posterior surface lateral to the apex of the glossal groove as in most forms with placoid flabella. Small disannular hairs on the anterior surface, often flattened and toothed at the apices, are limited to a narrow zone beyond the setae.

7.16 Beautifully cobblestoned posterior surfaces (curved over onto lateral surfaces) characterize the elongate flabella of the Ctenioschelini (Fig. 96E-G). The most peculiar feature of this tribe is the preapical, anterodistal projection, the postflabellum, extending beyond the apex of the main part of the flabellum (or preflabellum), and bearing several short setae on its posteroapical margin; a few small setae also arise laterally among the small, simple, disannular hairs of the anterior surface of the preflabellum.

7.17 An elongate (about as long as the flabellum), preflabellar, nonannular zone, hairless except for setae, characterizes Xylocopa (Fig. 99A, B), Bombini, and the Euglossini (Fig. 100). The setae in Xylocopa form a row across the apex of this zone on the anterior side, while in Bombini and Euglossini there are several setae scattered on both surfaces of this zone. The flabellum is elongate in Euglossini, a little longer than broad in Xylocopa, and its posterior surface with a cobblestone pattern at least distally. Its anterior surface bears numerous small, simple, disannular hairs but no setae. The apical margin is irregularly, weakly lobed in Eufriesea, simple or essentially so in other Euglossini and in Xylocopa.

7.18 In Anthophora (including Micranthophora), Amegilla, and Clisodon the flabellum is distinct, elevated basally above the level of adjacent glossa, often curled anteriorly at the sides giving a falsely elongate appearance, at least in dry specimens. Except in Clisodon and

some species of Anthophora the apex has one to several deep sinuses, forming elongate lobes (Fig. 95A-C). The small, simple, disannular hairs of the anterior surface are usually rather sparse. Setae are absent on or close to the flabellum, but are scattered among the annular hairs on the posterolateral surfaces of the glossa from the level of the apex of the glossal groove basad.

7.19 Finally, in Tetrapedia (Fig. 93A, D-F) the elongate, rather thick flabellum is smooth on its posterior surface, with a series of setae around its apex and with small simple hairs on the anterior surface. Thus these small hairs, instead of being distal to the row of setae as in the many other forms having such a row, are basal to the setae. If the setal row is homologous to the usual one, then the usual flabellum has been lost and is replaced by a presetal enlargement, but if the small hairs are homologous to the usual ones and in the usual position, then the setal row is a new development or has migrated distad.

SYSTEMATIC CONSIDERATIONS

No changes in taxonomic positions are made in this paper. Such changes should be based on consideration of all known characters, not merely on glossal attributes. Some taxa discussed below can readily be characterized by glossal characteristics. Others contain genera having such diverse features that characterization of higher taxa is impossible, a situation that in some cases may indicate lack of close relationship among included genera. The numbers refer to the paragraphs of the Comparative Account, where more details are provided.

FAMILY STENOTRITIDAE
(Figs. 39, 40)

Glossa short, thick, scarcely exceeding paraglossae, rounded, without distal specialization except that some bifid hairs are intermixed among simple ones. Disannulate surface as broad as annulate surface, hairy (5.1) except for triangular basal, median, bare area; hairs with tendency to be in longitudinal bands. Setae sparsely scattered among hairs of posterior surface and laterally among annuli of anterior surface. Annular hairs short, capitate, ending bluntly or truncate as in Colletidae (3.3); but annuli coarse, not fine and close as in most colletids (Figs. 30, 40).

The glossa is not as different from that of colletids as McGinley (1980) believed. Among the longest hairs on the glossa are those at its apex; these are disannular hairs like those of the glossal brush of colletids, and some are bifid, suggesting the branched hairs of the colletid glossal brush. McGinley correctly noted that the basiglossal sclerite of stenotritids is divided medially, forming two sclerites. However, contrary to his observations, the same is true of many colletids (Colletinae, Diphaglossinae and Hyleoides in the Hylaeinae), so that this character is not unique to stenotritids. It is, in fact, a feature of those colletids that have a broad glossa and fold it longitudinally when it is retracted.

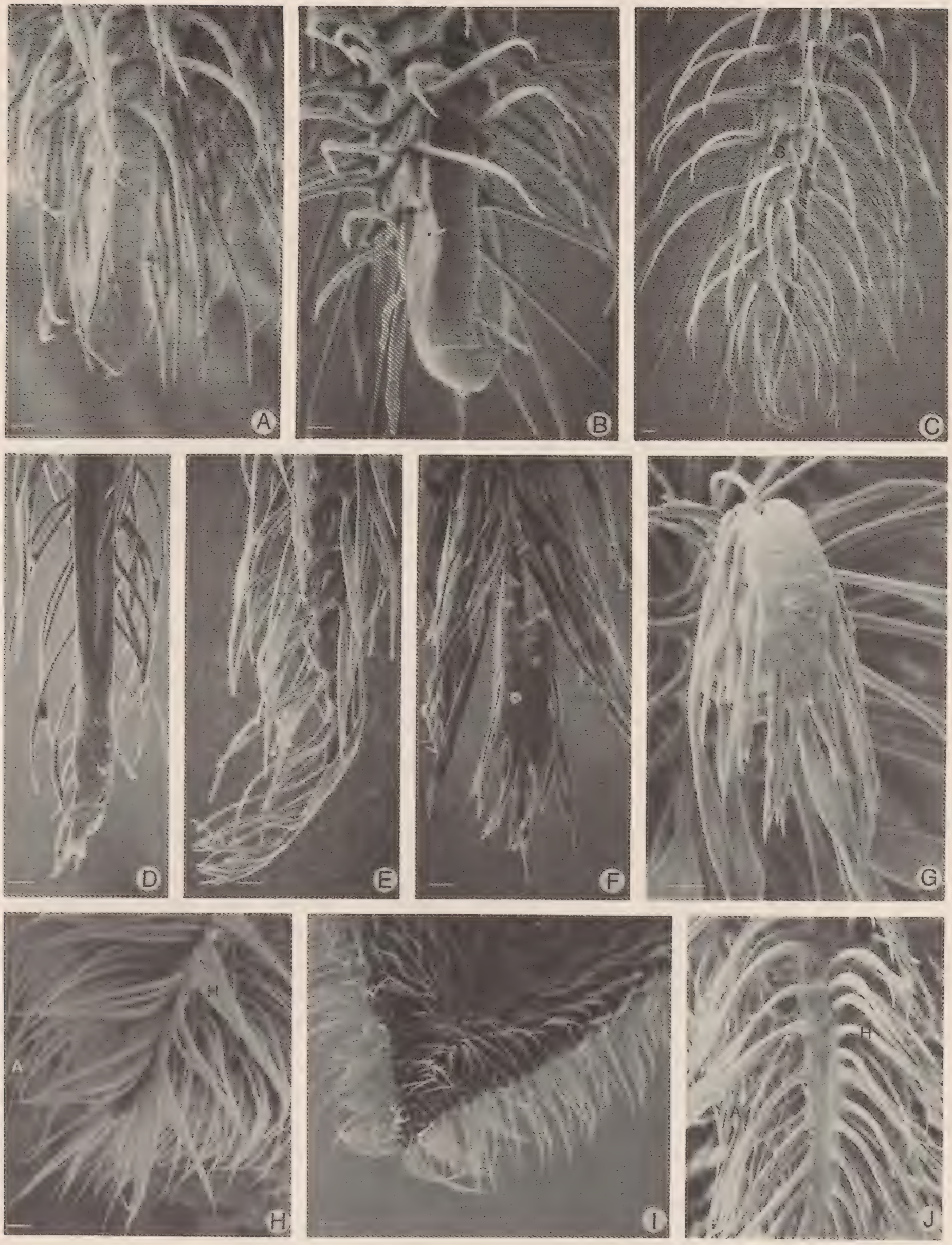


Figure 38. Apices (and preapical part, J) of glossae of Dufoureinae (Halictidae) and Andreninae. Scale lines represent .01 mm;

Species studied: Ctenocolletes smaragdinus (C); Stenotritus sp. (C).

FAMILY COLLETIDAE
(Figs. 1-3, 12-21)

Glossa short, truncate, bilobed, or bifid (but see next paragraph). Disannulate surface as broad as annulate surface because marginal lines are lateral; disannulate surface forming pair of large, apical, glossal lobes which bear conspicuous, branched or simple hairs forming the glossal brush (5.1); largely because of these glossal lobes, apex of glossa truncate or usually bilobed (1.2, 6.3), lobes long, attenuate, and directed laterad in Diphaglossinae; rest of disannular surface hairy or with substantial hairy areas (5.1). Setae forming transverse row across anterior surface basal to preapical fringe, but hidden by annular hairs, usually visible in cleared material from posterior view; setal row usually broken medially, represented only by one or two setae at extreme sides in some forms (e.g., Amphylaeus), and setae apparently absent in Chilicola and Palaeorhiza. Diphaglossinae also with some setae on posterior side and on basal parts of glossal lobes. Annuli, or one series of them, usually fine and close; annular hairs usually minute, their ends blunt or capitate (Fig. 11B-D); annular surface ending at preapical fringe (Figs. 1, 11C, D).

Almost none of the above listed characters apply also to males of Meroglossa and Palaeorhiza (6.5). They have a pointed glossa without glossal lobes (Figs. 16, 19); the disannular surface is narrower than the annular surface and the seriate hairs are large (5.6) but the disannular surface is otherwise bare. In these features they resemble the Halictidae. In males of Amphylaeus, also, the glossa is not bilobed, but has a small, hairy, median, apical projection of presumably disannulate origin, although it shows annuli (6.2, 6.3; Figs. 12, 13).

Because the colletid glossa is treated by McGinley (1980 and in prep.), minimum attention is paid to it in this paper.

Species studied: Colletinae. Colletes inaequalis (C), thoracicus (C, SEM); Leioproctus caerulescens (SEM), erythrogaster (SEM), herbsti (C); Lonchopria similis (SEM); Parapolyglossa sp. (C); Scrapter sp. (C, SEM). Diphaglossinae. Cadeguala occidentalis (C); Caupolicana hirsuta (C); Diphaglossa gayi (C); Policana albopilosa (SEM); Ptiloglossa guinnae (C). Euryglossinae. Brachyhesma incompleta (C); Euryglossa subsericea (SEM); Euryglossula chalcosoma (C); Hyphesma sp. (C). Hylaeinae. Amphylaeus morosus (C, SEM). Hylaeus basalis (SEM), episcopalis (SEM); Meroglossa torrida (C, SEM); Palaeorhiza parallela (C). Xeromelissinae. Chilicola ashmeadi (C, SEM).

H = seriate hair, A = annular hair, S = seta. A, B, C, Rophites trispinosus, anterior, posterior, and lateral views. D, E, Systropha curvicornis, posterior and lateral views. F, Dufourea marginata, posterior view. G, Same, apical view, apex curved anteriorly so that view is posterior for apex proper. H, I, Andrena erythrogaster, posterior and anterior views. J, Andrena helianthi, posterior view of preapical part.

FAMILY HALICTIDAE
(Figs. 4-6, 22-32)

Glossa short to rather long, tapering to attenuate apex, without flabellum, with weak apical enlargement in some Dufoureinae (6.7). Disannulate surface somewhat narrower than annulate surface because marginal lines are on posterior lateral surfaces of glossa (2.2), or narrowed to a median posterior line along much of glossa (Figs. 22, 31H). Disannular surface largely bare but seriate lines usually with long hair (5.7). Setae absent, a few among annular hairs in Rophites.

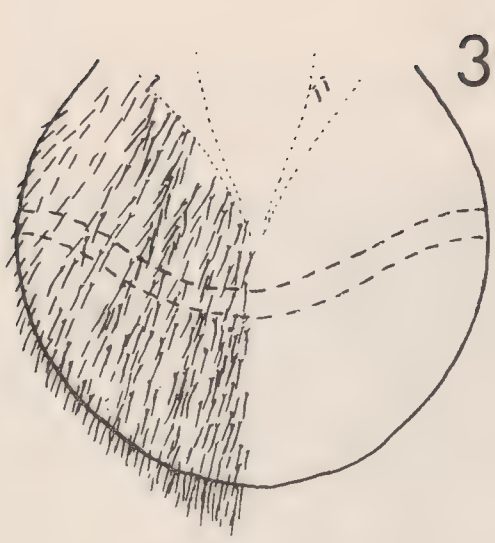
Subfamily Halictinae (tribes Augochlorini, Halictini, and Nomioidini). Annular hairs tapering to near apices, there abruptly broadly expanded or abruptly, divergently bifid, trifid, etc. (3.4, Fig. 31). Seriate hairs long (shortest in Corynura), sometimes simple except near apex of glossa (as in Sphecodes, Halictus, etc., Figs. 22, 31D), often broad-based and branched especially near apex of glossa, such hairs sometimes continued almost to glossal base as in Pseudaugochloropsis (Fig. 26) but more often replaced by simple hairs basally; seriate lines fused distally (5.7, 5.8) and sometimes (Pseudaugochloropsis) almost to base of glossa (Figs. 22, 31H).

Species studied: Augochlorini. Augochlora pura (C, SEM); Augochlorella striata (C), persimilis (SEM); Augochloropsis metallica (C, SEM); Corynura chilensis (C), chloris (C); Megalopta genalis (C, SEM); Neocorynura pubescens (C, SEM); Paroxystoglossa transversa (C, SEM); Pseudaugochloropsis graminea (C, SEM); Temnosoma metallica (C, SEM). Halictini. Agapostemon radiatus (SEM), texanus (C); Caenohalictus azarae (C); Habralictus trinax (C); Halictus hesperus (C), ligatus (C, SEM), maculatus (C), quadricinctus (C); Lasioglossum calceatum (C), imitatum (C), leucozonium (C), lustrans (C, SEM), nigripes (C), rohweri (SEM), sisymbrii, texana (C, SEM); Pseudagapostemon divaricatus (SEM), Pseudagapostemon sp. (C); Ruizantheda mutabilis (C); Sphecodes gibbus (C, SEM); Thrinchostoma producta (SEM), Thrinchostoma sp. (C); Zonalictus sp. (SEM). Nomioidini. Nomioides divisa (SEM), minutissima (C).

Subfamily Nomiinae. There are striking differences between the two subgenera of Nomia examined, Acunomia and Epinomia, supporting the view expressed elsewhere (Michener, 1965) that these subgenera should probably be placed in separate genera.

Annular hairs mostly simple, some bifid near apex of glossa (Acunomia) or mostly rather abruptly bifid (Epinomia) (3.4, Fig. 32H, I). Seriate ridges weak, hairless except for small, branched seriate hairs at apex of glossa (Acunomia, Fig. 28), these ridges separate nearly to apex of glossa; alternatively, seriate hairs large, mostly trifid or bifid, present only near apex of glossa (Epinomia, Fig. 30), seriate ridges fused in distal third or fourth of glossa and otherwise absent.

Figures 39-50. Diagrams of posterior surfaces and cross-sections of glossae of Stenotritidae, Oxaeidae, and Andrenidae. 39, 40. Stenotritus elegans. 4l, 42. Protoxaea gloriosa. 43, 44. Andrena helianthi. 45, 46. Pseudopanurgus aethiops. 47, 48. Calliopsis andreniformis. 49, 50. Melitturga clavicornis. Explanation as for Figures 22-30.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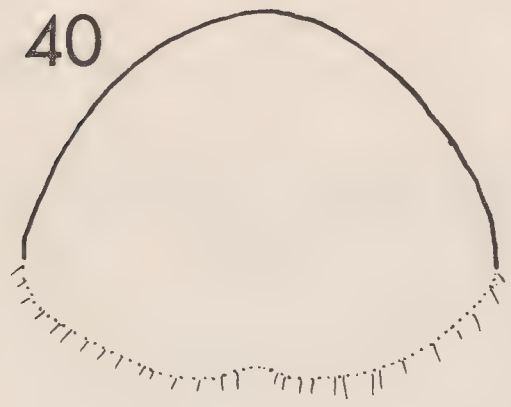
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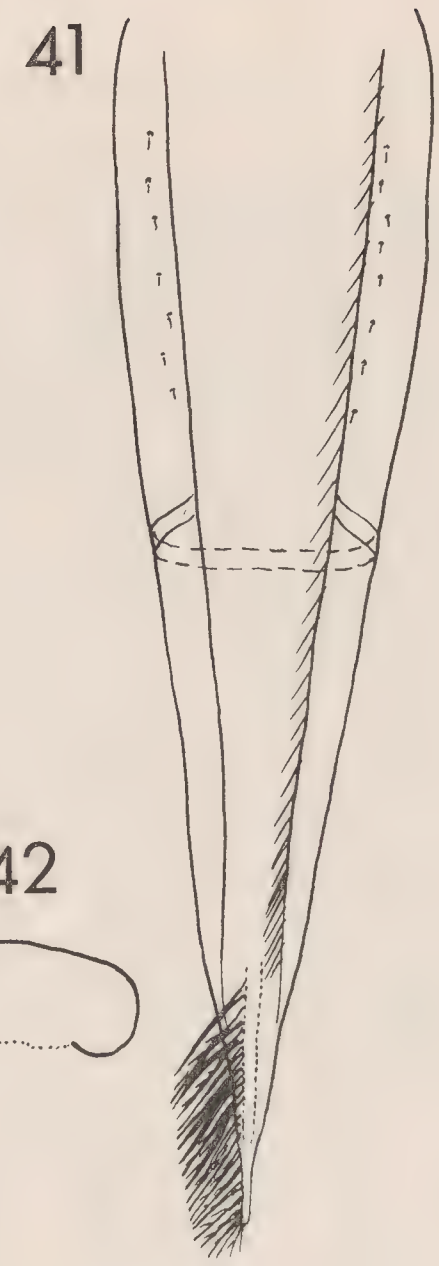
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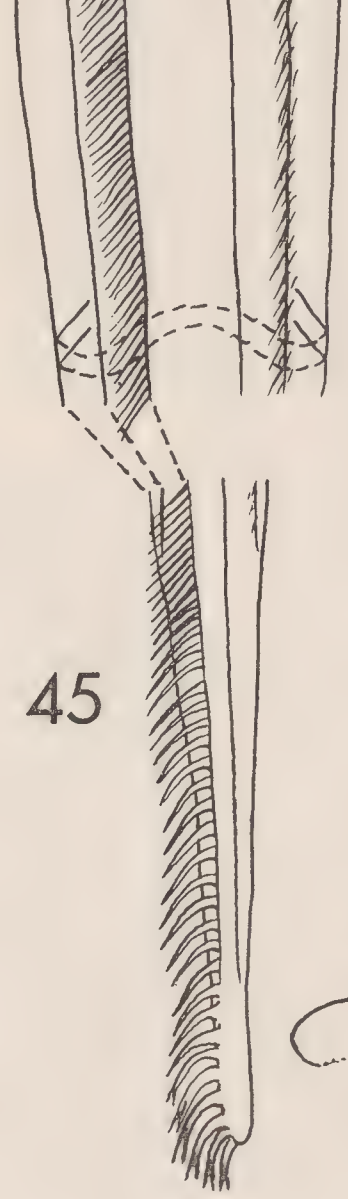
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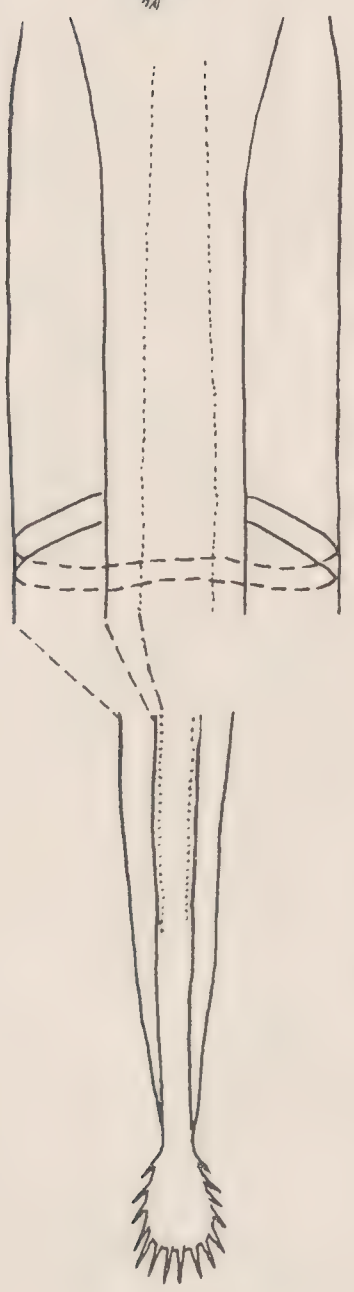
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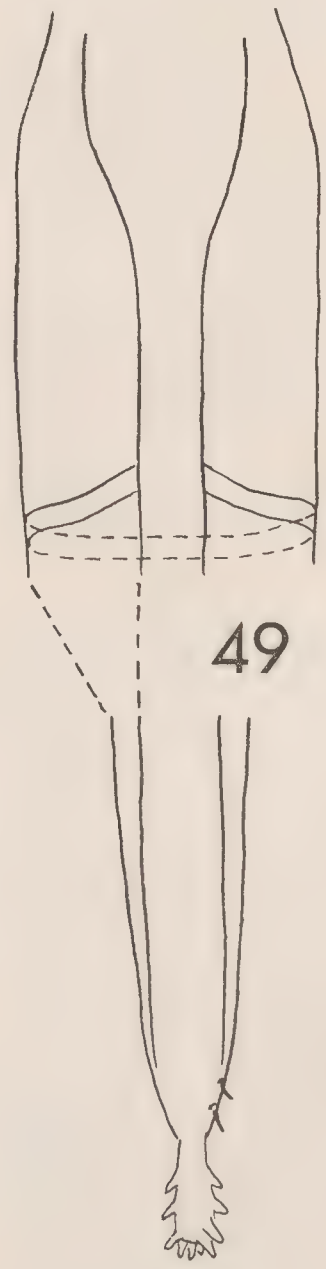
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Species studied: Nomia melanderi (C), nevadensis (C, SEM), nortoni (SEM).

Subfamily Dufoureinae. Annular hairs usually slender, tapering, sometimes slender lanceolate (3.4), in Dufourea hairs of middle annuli abruptly bifid, more distal ones expanded apically with several teeth. Seriate hairs short and sparse, present only on basal half of glossa (Systropha), moderately long and simple (Rophites and Micralictoides) or long, some with a short branch (Dufourea). Seriate ridges separated nearly to apex (Figs. 33-37). In Rophites and Systropha there is a glossal thickening which suggests a glossal rod (4.3) and a suggestion of such a thickening is sometimes visible in the distal part of the glossa of Dufourea. Distal specialization as described in 6.7 (Fig. 38A-G) (absent in Micralictoides).

Although as indicated in the illustrations, there is considerable variation in the Dufoureinae, this subfamily shows some distinctive common features, several of them shared with the Nomiinae and with Halictinae. Especially noteworthy are the abruptly bifid, trifid, or expanded apices of at least some of the annular hairs in Dufourea. Other genera of Dufoureinae are different in various ways and would not necessarily have been placed in the Halictidae on the basis of glossal characters.

Species studied: Dufourea marginata (C, SEM); Micralictoides altadenae (C); Rophites quinquespinosus (C), trispinosus (SEM); Systropha curvicornis (C, SEM).

FAMILY ANDRENIDAE
(Figs. 38H-J, 43-52E)

Glossa short and tapering (Andrena, Figs. 38I, 43; Epimethia) to rather long (1.5) and sometimes parallel-sided except distally, apex attenuate, with or without flabellum. Disannulate surface largely bare, narrower than annulate surface because marginal lines are on posterior lateral surface of glossa; in a few genera marginal lines close together on posterior surface of glossa (2.2) and in Melitturga (Fig. 49) so close, and with the surface between them so invaginated, as to delineate a glossal groove. Marginal line and seriate line of each side sometimes approximate or apparently fused so that annuli reach or nearly reach seriate lines (2.5); marginal and seriate hairs in such areas become indistinguishable. Flabellar presence (7.1-7.5) not necessarily a generic character, thus distinct in most species of Perdita but scarcely recognizable in P. maculigera and totally absent in P. texana; distinct in Nomadopsis zebrata but absent (merely an attenuate apex, without basal constriction) in N. scutellaris. Glossal apex without setae except in Arhysosage, Perdita, and Callonychium (7.7) and perhaps Camptopoeum and

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Figure 51. Apices of glossae of Panurginae (Andrenidae). Scale lines represent .01 mm; H = seriate hair. A, B, Protandrena bancrofti, anterior and posterior views. C, Heterosarus illinoiensis, posterior view. D, E, Panurgus calcaratus, posterior views. F, G, Calliopsis andreniformis, posterior and anterior views. H, Calliopsis coloradensis, anterior view. I, Liopoeum trifasciatum, posterolateral view. J, Nomadopsis australior, posterior view.


A


H
B


H
C


D


E


F


G


H


I


J

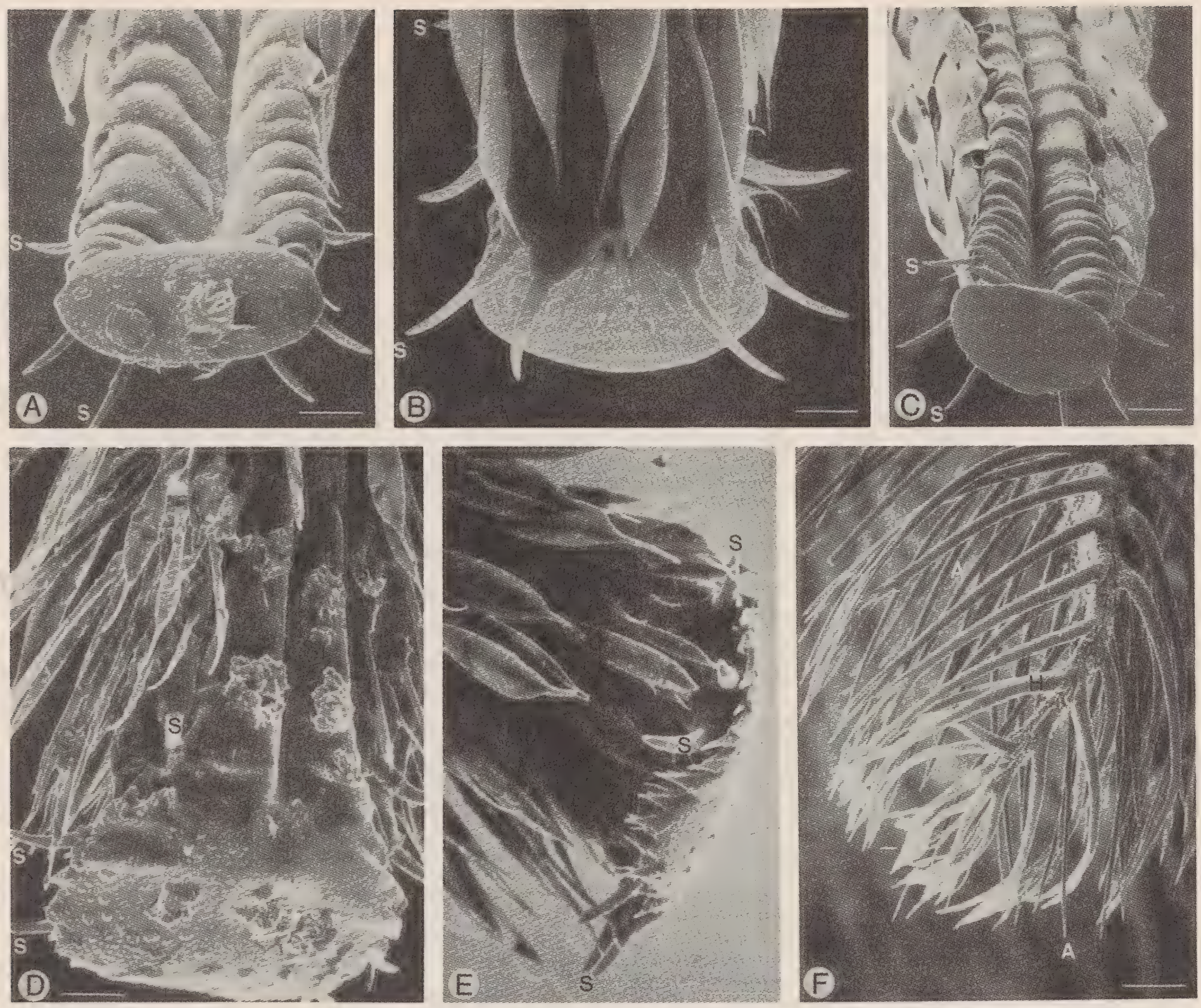


Figure 52. Apices of glossae of Panurginae (Andrenidae) and Oxaeidae. Scale lines represent .01 mm; H = seriate hair, A = annular hair, S = seta. A, B, Perdita zebrata zebrata, posterior and anterior views. C, Perdita tridentata, posterior view. D, E, Callonychium flaviventre, posterior and anterior views. F, Mesoxaea nigerrima, posterior view.

Plesiopanurgus (6.8). Annular hairs usually slender and tapering, rarely narrowly lanceolate on distal part of glossa (e.g., in Panurginus polytrichus but not occidentalis, Protandrena bancrofti but not mexicana), largely lanceolate in some species of Perdita (3.1).

Interesting features of certain groups are as follows: A group of presumably primitive forms (6.5) have the seriate hairs of most of the glossal length simple and slender (5.5) but those of the distal part of the glossa coarse, bifid or sometimes with more branches, resembling those of Halictinae. Such forms are Andrena helianthi (Fig. 43) (not A. erythrogaster in which the seriate hairs are either simple or split to their bases, Fig. 38H), Pseudopanurgus (Fig. 45), Xenopanurgus, Panurginus, Protandrena (Fig. 51B), Pterosarus, Heterosarus, Psaenythia, and Metapsaenythia. The two series of seriate hairs are well separated, joined only near the extreme apex of the glossa, leaving an elongate,

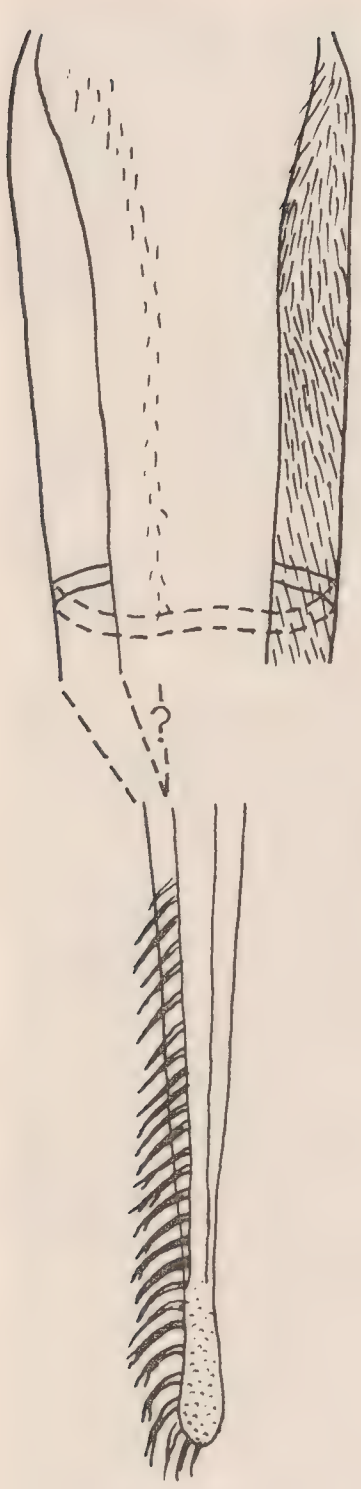
bare, apical area, sometimes narrow, on the posterior surface of the glossa. Similar glossal apices with large seriate hairs, but these hairs mostly simple, are found in Cephalurgus, Liphanthus, and Epimethia. In Panurgus the basal third of the glossa is similar to that of Pseudopanurgus (Fig. 45), but the rest has the seriate hairs closely associated with the marginal hairs, and the space between the seriate lines cobblestoned, slightly strengthened (4.4), broad and concave all the way to the apex so that the apical region is not differentiated, with the disannular hairs at the apex minute and simple (Fig. 51D, E). Panurgus also has two or three setae scattered among the annular hairs laterally, on the apical part of the glossa.

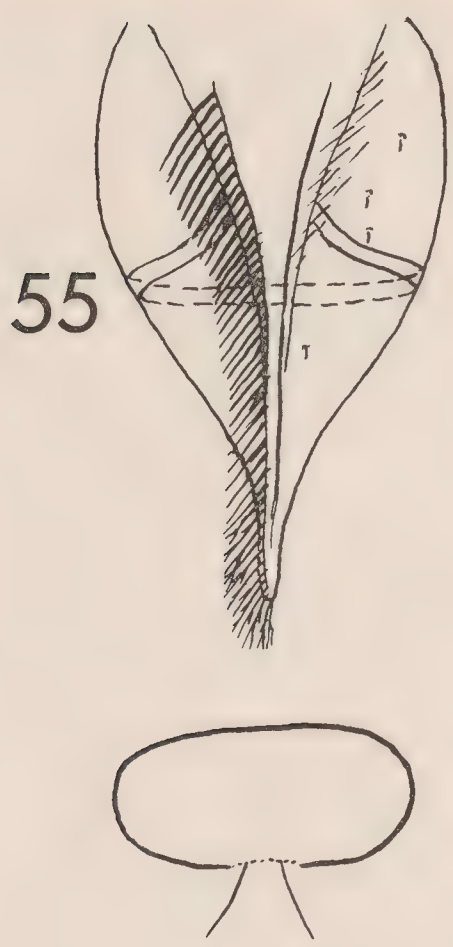
In a considerable group of genera such as Calliopsis (Fig. 47), Nomadopsis, Hypomacrotera, Spinoliella, Arhysosage, Liopoeum, and Acamptopoeum there appear to be no disannular hairs except for small ones preapically (Fig. 51J) and around the edges of the flabellum or its equivalent (6.6). (It is often difficult to distinguish a finely wrinkled disannular surface from a series of hairs. We believe, however, that hairs are absent in all of these genera except near the glossal apex.) The distal specialization, as in the preceding groups, does not usually involve recognizable setae. In Hypomacrotera and Nomadopsis scutellaris there are long, marginal hairs around the attenuate apex which is bare on the posterior surface. In Spinoliella and Arhysosage these hairs are reduced to small spicules and in Arhysosage there are four setae on the anterior surface near the apex. In Acamptopoeum and Liopoeum hirsutulum a preapical constriction differentiates an elongate flabellum which bears small spicules similar to those of Spinoliella; setae are absent. Finally, in Calliopsis, Liopoeum trifasciatum, and Nomadopsis zebrata, there is a well formed flabellum with long marginal processes or hairs (Fig. 51F-J).

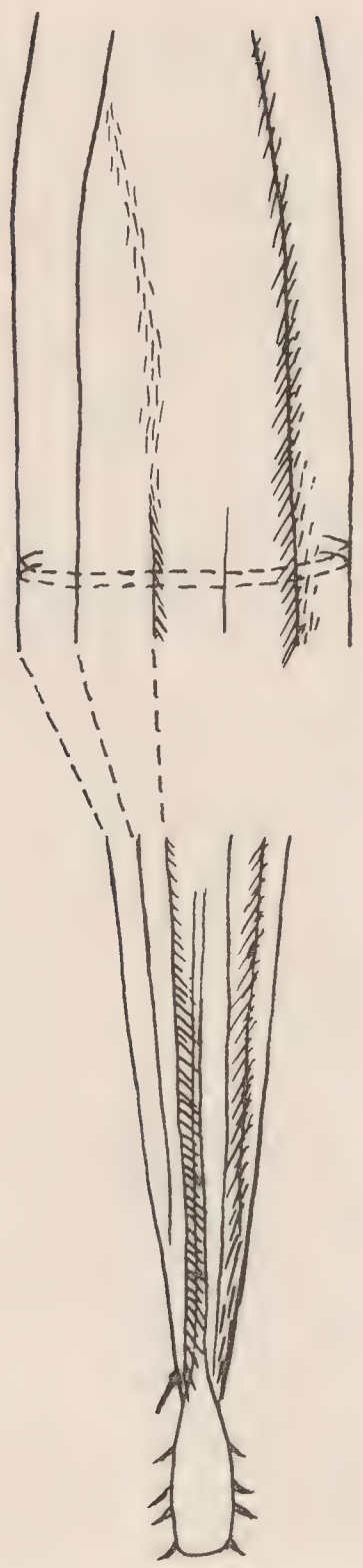
Melitturga also lacks seriate hairs. The glossa is elongate and tubular, with an elongate flabellum similar to that of Acamptopoeum but with the spicules coarse and blunt (Fig. 49), the anterior side with a few small hairs. A few setae are among annular hairs at the sides, basal to the flabellum.

In Callonychium and Perdita (Fig. 52A-E) there are distinct preapical setae. Except for some species of Perdita, there is a distinct, transverse flabellum, the margin of which has small, sharp projections or spicules in Callonychium but is smooth in Perdita. The flabellum is placoid, similar to that of many long-tongued bees, even to the presence across its base on the anterior surface of a series of several setae. In Perdita (5.9) the seriate lines are broad and rounded, each divided by grooves into a series of transverse, rounded ridges. These ridges probably represent expanded bases of seriate hairs for (except in P. texana) each tapers laterally into a short hair or point. In P. texana the basal parts of the seriate ridges are not transversely ridged, but bear scattered (i.e., not in a row), short seriate hairs.

A weak glossal "rod" appears in some preparations of Calliopsis, Panurgus, etc. This is a weak integumental thickening or darkening, sometimes flat and sometimes a trough resulting from the meeting of sloping planes of the integument (4.3, 4.4).







Figures 53-58. Diagrams of posterior surfaces and cross-sections of glossae of Melittidae and Ctenoplectridae. 53, 54. Dasypoda panzeri. 55, 56. Macropis europaea. 57, 58. Ctenoplectra fuscipes. Explanation as for Figures 22-30.

Species studied: Andreninae. Ancylandrena larreae (SEM); Andrena erythrogaster (C, SEM), halli (SEM), helianthi (C, SEM), illinoiensis (C, SEM), miserabilis (SEM), nigrae (SEM), perplexa (SEM), prunorum (SEM); Megandrena enceliae (SEM). Panurginae. Acamptopoeum pruni (C); Arhysosage ochracea (C); Calliopsis coloradensis (SEM), andreniformis (C, SEM); Callonychium flaviventre (SEM); Camptopoeum frontale (SEM); Heterosarus illinoiensis (SEM), neomexicanus (C); Hypomacrotera subalpinus (C, SEM); Liopoeum trifasciatum (SEM); Melitturga clavicornis (C, SEM); Meliturgula sp. (C); Metapsaenythia abdominalis (C); Nomadopsis australior (SEM), scutellaris (SEM); Panurginus occidentalis (SEM), polytrichus (SEM); Panurgus calcaratus (C, SEM); Perdita acapulcona (C), albipennis (C), bishoppi (C), maculigera maculipennis (C), texana (C), tridentata (SEM), zebrata zebrata (SEM); Protandrena bancrofti (SEM), mexicana (SEM); Psaenythia bergi (C); Pseudopanurgus aethiops (C), herbsti (SEM); Pterosarus ornatipes (SEM).

FAMILY OXAEIDAE
(Figs. 41, 42, 52F)

Glossa rather short, tapering to an attenuate apex, without flabellum. Disannulate surface largely bare (Fig. 41), narrower than annulate surface because marginal lines are on posterior lateral part of glossa. Marginal hairs present (probably all annular hairs); seriate hairs large and branched, present only on distal part of glossa (5.4). Median and basal part of glossa with peg-like setae scattered among posterior extremities of annuli. Distal part of glossal surface and bases of seriate hairs with surfaces (Fig. 52F) finely granular or "mealy." Annular hairs simple, tapering.

The only character that distinguishes the glossa consistently from that of melittids, andrenids, and the few halictids with simple annular hairs, is the presence of setae in its median and basal part. Among other short-tongued bees, setae are present in Stenotritidae, Colletidae, and in a few dufoureine and panurgine genera.

Species studied: Mesoxaea nigerrima (SEM); Oxaea flavescens (SEM); Protoxaea gloriosa (C, SEM).

FAMILY MELITTIDAE
(Figs. 53-56, 59A-E, G, H)

Glossa short (Macropis, Fig. 55) to moderately elongate, tapering, apex attenuate, without flabellum although with gradually broadened apex in Dasypoda (6.5, Fig. 59A). Disannulate surface largely bare, narrower than annulate surface because marginal lines are on posterior lateral surfaces of glossa. Marginal hairs often abundant, especially basally. Seriate hairs distinct on distal part of glossa, moderately large, at least distal ones branched. Basad, seriate hairs long and simple, and seriate lines diverging from marginal hairs in Macropis (Fig. 55); in others seriate hairs absent basally (possibly indistinguishable from innermost marginal hairs), or small as in Meganomia or minute as in Dasypoda. On distal attenuate part of glossa, seriate lines and therefore bases of seriate hairs adjacent (Fig. 59C, H) or separated so that elongate smooth or "cobblestoned" strip is present, basal to which seriate lines (if recognizable) are usually close together for some distance before diverging basally. Setae absent or in Macropis scattered among annular hairs on lateral and anterior surfaces. Annular hairs simple, tapering.

There are no consistent familial characters by which the melittid glossa differs from that of Andrenidae, etc. Dasypoda and Meganomia are unusual in that there are two longitudinal bands of small to minute hairs on the basal part of the disannulate surface. These hairs do not intergrade with the large seriate hairs on the distal part of the glossa. If, as seems likely, the small or minute hairs are seriate hairs, then seriate hairs and lines are simply absent on the basal part of the glossa except in Macropis, Dasypoda, and Meganomia.

Species studied: Meganomiinae. Meganomia gigas (C, SEM). Melittinae. Macropis europaea (C, SEM); Melitta leporina (C), tricincta (SEM). Dasypodinae. Capicola braunsiana (SEM); Dasypoda panzeri (C, SEM); Haplomelitta ogilviei (SEM); Hesperapis carinata (SEM), pellucida (C).

Figure 59. Apices of glossae of Melittidae and Ctenoplectridae. Symbols as in Figure 52. A, B, Dasypoda panzeri, posterolateral and posterior views. C, Melitta tricincta, posterior view. D, Dasypoda panzeri, anterior view. E, Hesperapis carinata, posterior view. F, Ctenoplectra albolimbata, lateral view. G, H, Meganomia gigas, posterior views. I, Ctenoplectra albolimbata, posterior view.

FAMILY CTENOPLECTRIDAE
(Figs. 57, 58, 59F, I)

Glossa moderately elongate, tapering, apical part not conspicuously attenuate, its narrowing being continuous with that of rest of glossa; flabellum present, longer than broad (sometimes much longer), weakly constricted at base, annuli present on its anterior surface (7.1). Disannulate surface considerably invaginated (Fig. 58), largely bare, narrower than annulate surface because marginal lines are on posterior lateral surfaces of glossa. Annuli often not reaching marginal lines; seriate lines well separated from marginal lines, with converging short, fine, simple seriate hairs, not enlarged toward glossal apex, not evident in flabellar area. Flabellum with a few tapering setae on lateral margins of anterior surface, extending laterally beyond sometimes toothed or lobed lateral flabellar margins; preapically two or four setae forming row across flabellum on anterior surface; a seta on each side basal to flabellum on posterior lateral surface of glossa. Annular hairs slender, tapering, some distal hairs (marginal or annular) in some species broadened, bifid or trifid.

Other ctenoplectrid characters in agreement with those of long-tongued bees are listed by Michener and Greenberg (1980). The same authors illustrate some of the variation in flabellar structure within the genus Ctenoplectra.

Species studied: Ctenoplectra albolimbata (C, SEM), fuscipes (C), bequaerti (C).

LONG-TONGUED BEES
(Figs. 7-10, 60-101)

Members of this group, which includes the families listed below, share numerous characteristics of the glossa, if various parasitic forms are ignored. The characters listed here are those of nonparasitic forms, although comments on parasitic groups are incorporated into accounts of the relevant taxa.

Glossa elongate, commonly parallel-sided basally and tapering apically, not conspicuously attenuate, its narrowing being continuous with that of rest of glossa (1.3); flabellum present with a few exceptions, weakly to strongly constricted at base, usually without annuli on anterior surface. Disannulate surface of glossa, except at extreme base and apex, commonly invaginated to form glossal canal (4.2) which is sufficiently closed to form glossal groove, commonly filled by marginal hairs; seen externally, annuli usually seem to go all the way around glossa except for glossal groove (2.3); marginal hairs abundant, much smaller than most annular hairs, usually larger than seriate hairs; sclerotized but flexible glossal rod (4.4) in roof of glossal canal. (In prepared material and perhaps in life the canal is sometimes evaginated in middle part of glossa so that rod is exposed.) Seriate lines on or lateral to rod; seriate hairs (5.10) simple, usually minute, mostly directed mesodistally instead of laterodistally as in short-tongued bees, exposed and sometimes branched only at base of glossa and on anterior side of flabellum (if such hairs are correctly identified as seriate). Setae present, usually at base or anterior surface of flabellum, but sometimes only lateroposteriorly on glossa among annular

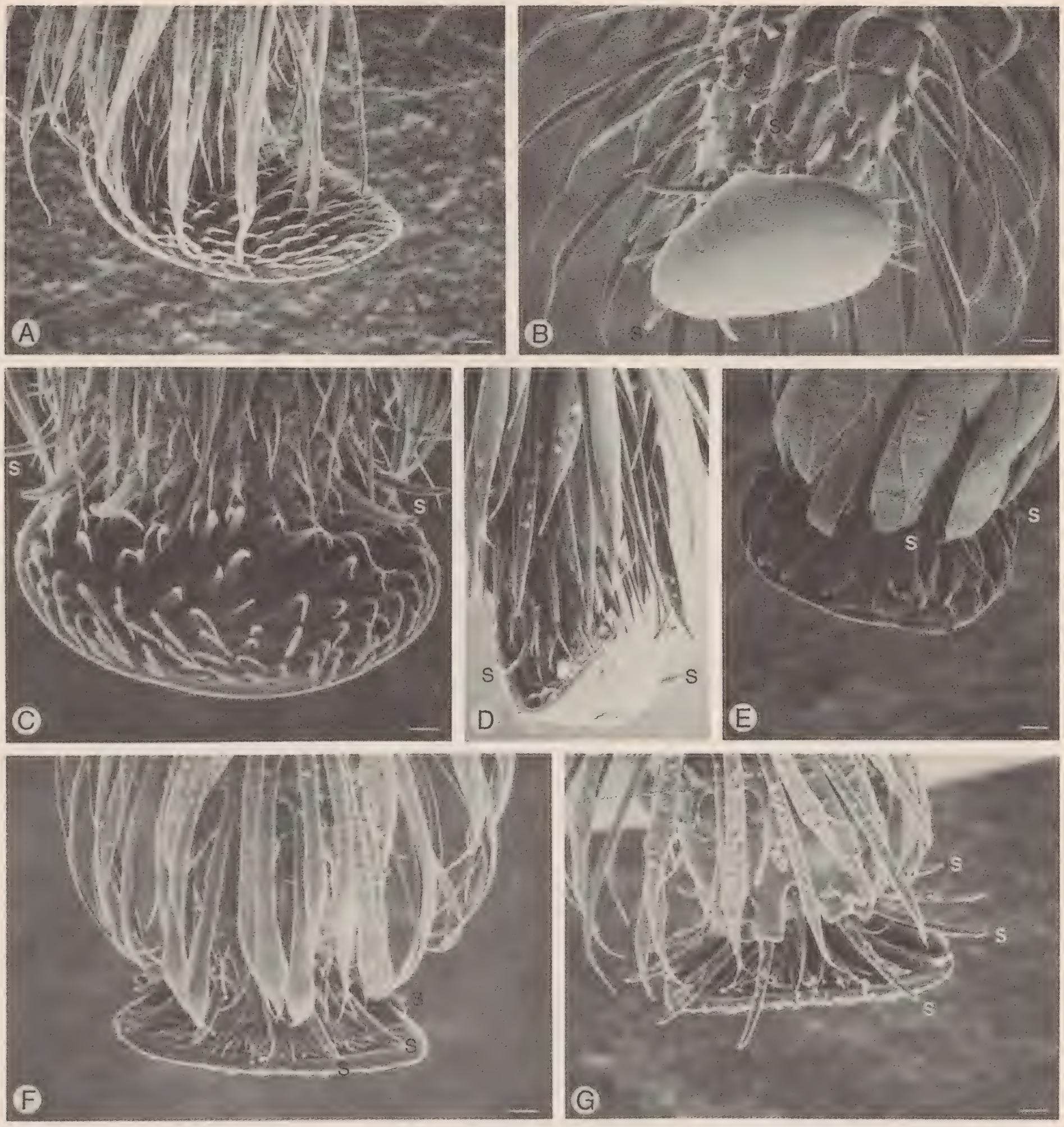


Figure 60. Apices of glossae of Fideliidae and Megachilidae. Scale lines represent .01 mm; S = seta. A, Parafidelia pallidula, anterolateral view. B, Neofidelia profuga, posterior view. C, Fidelia villosa, anterior view. D, Trichothurgus dubius, anterior view with flabellum curved so that posterior surface of its apex is visible. E, Trichothurgus wagenknechti, anterior view. F, Anthidium emarginatum, anterior view. G, Dianthidium curvatum sayi, anterior view.

hairs basal to flabellum; a few setae among annular hairs nearly always present. Annular hairs sometimes tapering, often lanceolate, sometimes in part expanded and scale-like.

FAMILY FIDELIIDAE
(Figs. 60A-C, 62)

In available preparations glossal groove open, fully exposing glossal rod and disannulate surface lateral to it (4.4). (If this is characteristic of the family, it must be a primitive feature.) Rod V-shaped in cross-section (Fig. 62), minute seriate hairs on ridges (seriate lines) formed by ends of "V." No other hairs on disannulate surface, but membrane minutely papillate in some areas. Flabellum placoid, rounded, broader than long, with numerous short unbranched hairs on anterior surface. Setae present basal to flabellum on both anterior and posterior surfaces (Fig. 60B), at least laterally, not forming complete row across base of flabellum. Annular hairs tapering (3.1) or very narrowly lanceolate.

The glossa sheds no new light on whether or not this family should be included within the Megachilidae; there are no glossal characters that clearly distinguish Fideliidae from Megachilidae.

Species studied: Fidelia villosa (SEM); Neofidelia profuga (C, SEM); Parafidelia pallidula (SEM).

FAMILY MEGACHILIDAE
(Figs. 60D-G, 61, 63-65)

Glossal rod U-shaped in cross-section (Lithurge, Hoplitis) or lenticular, seriate lines along summits of the U or as separate sclerotized ridges a short distance lateral from rod, so that there appear to be three rods (Fig. 65); seriate hairs minute, no other hairs on disannulate surface. Flabellum placoid, rounded, broader than long, posterior surface smooth, anterior surface concave, with short, unbranched hairs (or a few branched in some Anthidiini). A few setae scattered among annulate hairs on posterolateral surfaces of distal part of glossa. Several setae at level of base of flabellum at sides forming row (sometimes broken medially) across base of flabellum on anterior side (Figs. 60F, G; 61A, C), often (e.g., Hoplitis, Megachile, and Parevaspis) extending around onto posterior surface at base of flabellum (Fig. 61D, E). Annular hairs tapering or lanceolate.

Species studied: Lithurginae. Lithurge apicalis (SEM), gibbosus (C); Trichothurgus dubius (C, SEM), wagenknechti (C, SEM). Megachilinae. Tribe Anthidiini. Allanthidium (SEM); Anthidiellum (C, SEM); Anthidium (C, SEM); Aztecanthidium (C, SEM); Callanthidium (C, SEM); Capanthidium (SEM); Carinanthidium (SEM); Dianthidium (C, SEM); Euaspis (C, SEM); Heteranthidium (C); Hypanthidium (C); Immanthidium (C); Nananthidium (C); Notanthidium (C); Odontostelis (C); Pachyanthidium (C); Paranthidium (C); Parevaspis (C, SEM); Serapista (SEM); Spinanthidium (C, SEM); Stelis (C, SEM). Tribe Dioxyini. Dioxys (C, SEM). Tribe Megachilini. Anthocopa (C); Ashmeadiella (C, SEM); Chalicodoma (C); Chelostoma (C); Chelostomopsis (C); Coelioxys (C); Creightonella (C); Heriades (C, SEM); Hoplitis (C); Megachile (C, SEM); Noteriades (C); Osmia (C, SEM); Proteriades (C). (To save space, only the genera are listed for Megachilinae.)

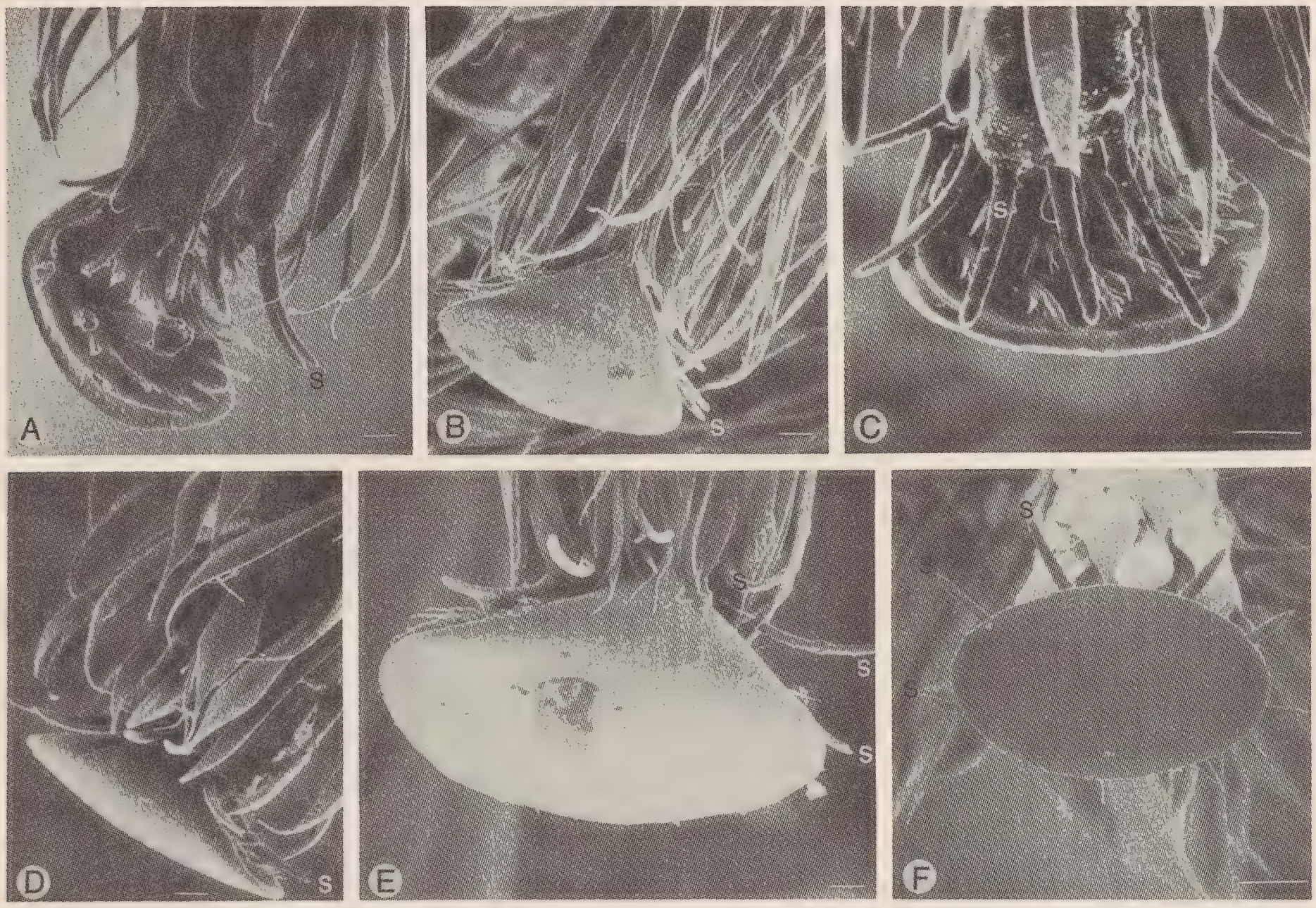


Figure 61. Apices of glossae of Megachilidae. Scale lines represent .01 mm; S = seta. A, Anthidiellum perplexum, anterolateral view. B, C, Spinanthidium volkmanni, posterior and anterior views. D, Parevaspis carbonaria, posterior view. E, Megachile melanophaea, posterior view. F, Ashmeadiella bigeloviae, anterior view.

FAMILY ANTHOPHORIDAE
(Figs. 66-85, 92-99, 1001)

This large family, like some of the included subfamilies, is diverse in glossal characteristics. Aside from the characteristics of long-tongued bees listed above, there are no unifying attributes of the glossae, and there exist parasitic anthophorids which do not agree with the features listed for long-tongued bees.

Subfamily Anthophorinae. Tribe Exomalopsini. Glossal rod rather flat or lenticular in cross-section (Fig. 67, 68); seriate lines near rod, forming distinct and sometimes high ridges; seriate hairs numerous and minute. Ends of annuli not reaching margins of glossal groove, some

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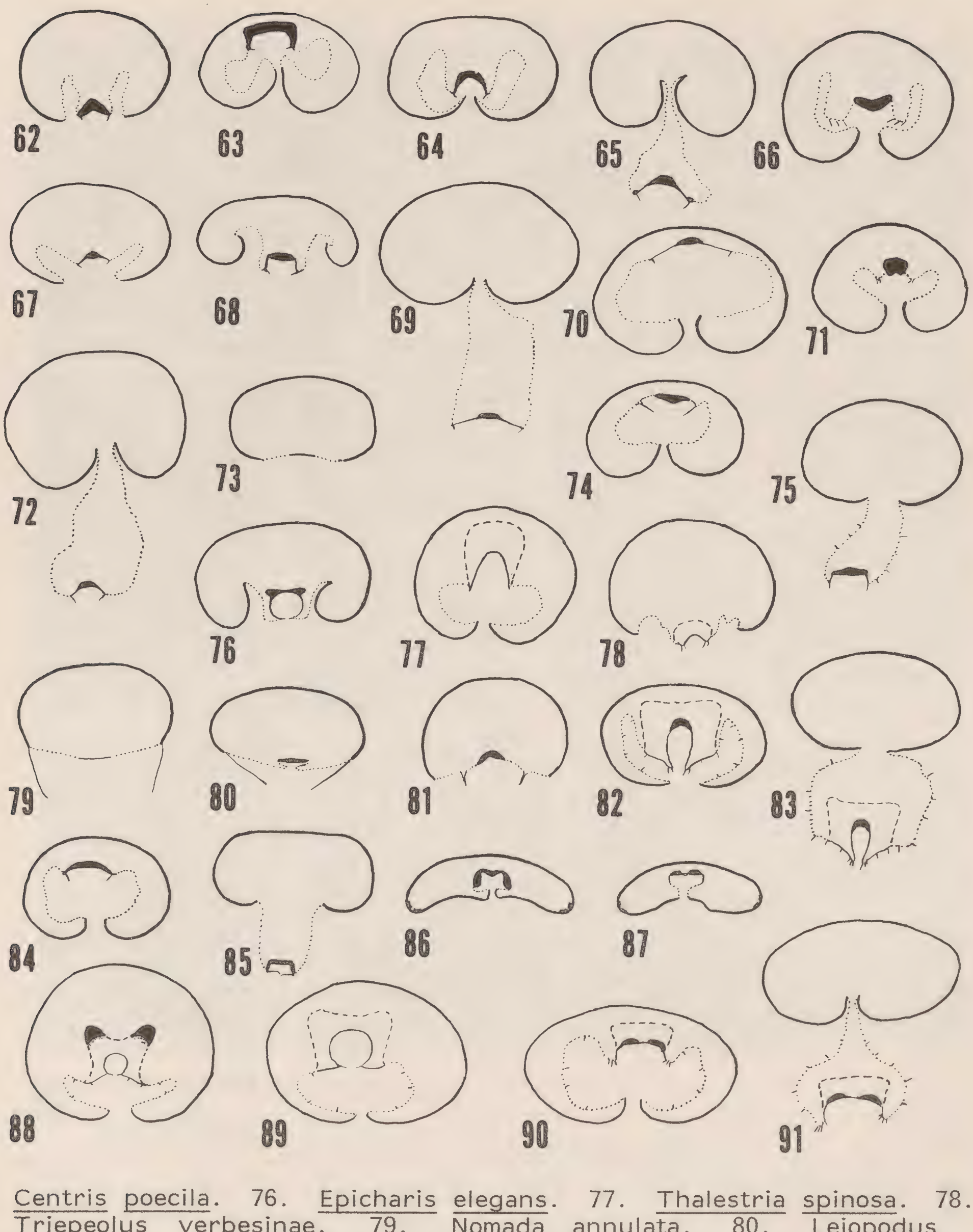
Figures 62-91. Cross-sections through median parts of glossae of long-tongued bees. 62. Neofidelia profuga. 63. Lithurge gibbosus. 64. Hoplitis albifrons. 65. Creightonella frontalis (rod everted). 66. Melitoma taurea. 67. Ancyloscelis panamensis. 68. Tapinotaspis caerulea. 69. Xenoglossa strenua (rod everted). 70. Same, rod not everted. 71. Canephorula apiformis. 72. Anthophora occidentalis (rod everted). 73. Xeromelecta californica. 74. Mesocheira bicolor. 75.



Centris poecila. 76. Epicharis elegans. 77. Thalestria spinosa. 78. Triepeolus verbesinae. 79. Nomada annulata. 80. Leiopodus lacertinus. 81. Isepeolus viperinus. 82. Xylocopa virginica. 83. Same (rod everted). 84. Ceratina laeta. 85. Macrogalea candida. 86. Eulaema cingulata (bases of large, lanceolate annular hairs at sides). 87. Eufriesea violacea (notation as for 86). 88. Melipona fasciata. 89. Apis mellifera. 90. Bombus pennsylvanicus. 91. Same (rod everted). Conventions are the same as for sectional diagrams, Figures 22-30.

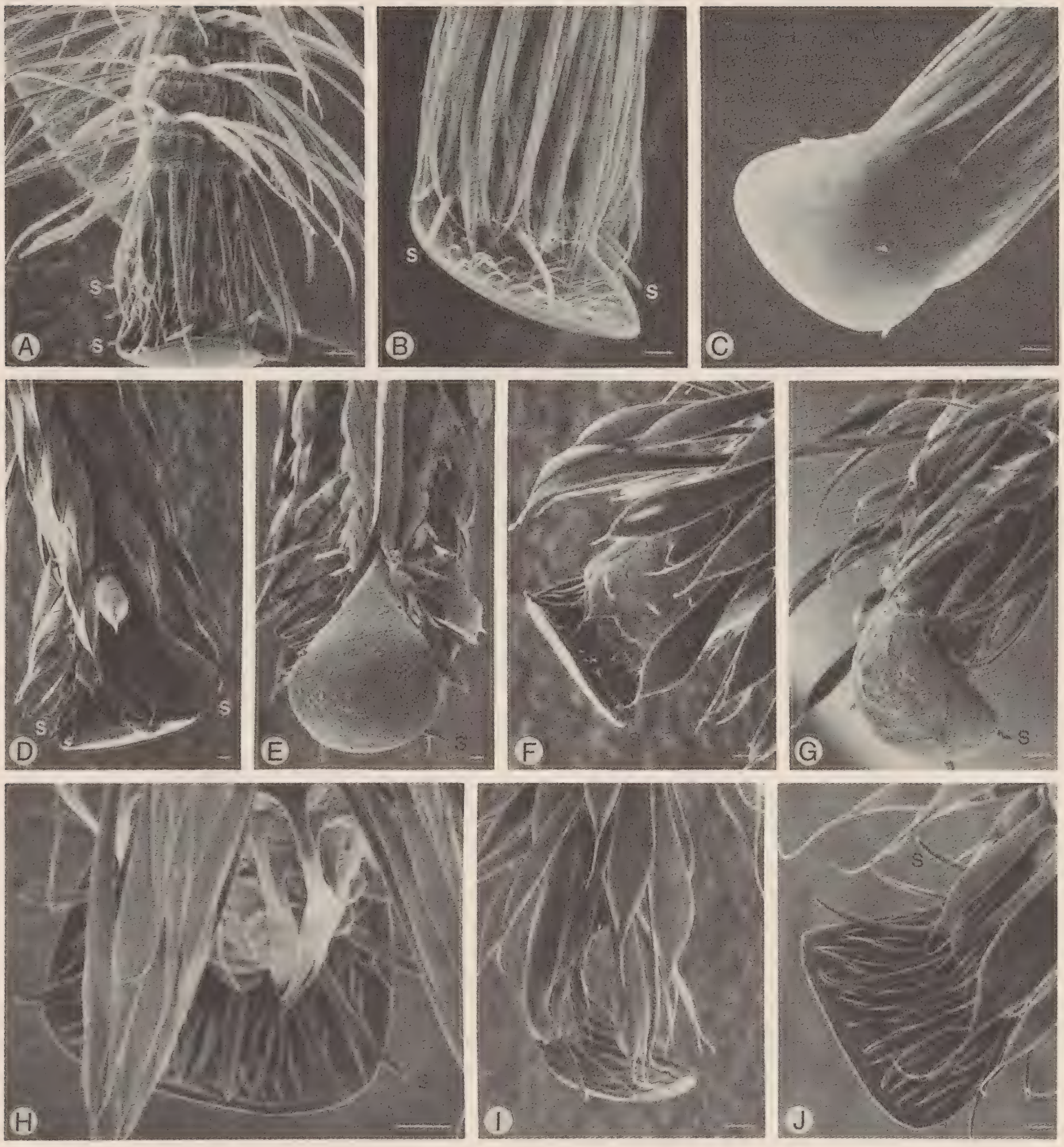


Figure 92. Apices of glossae of Exomalopsini (Anthophoridae). Scale lines represent .01 mm; S = seta. A, Exomalopsis solani, anterior view. B, C, Exomalopsis zexmeniae, anterior and posterior views. D, E, Ancyloscelis apiformis, anterior and posterior views. F, G, Caenonomada bruneri, anterior and posterolateral views. H, Tapinotaspis caerulea, anterior view. I, J, Paratetrapedia lugubris, anterolateral and anterior views.

small hairs usually scattered between ends of annuli and groove, as well as on surface in glossal canal (5.11) between seriate lines and margins of groove. Glossa only feebly narrowed at base of flabellum. Flabellum placoid, posterior surface smooth, margin simple, rounded or in

Paratetrapedia subtruncate but rounded laterally; anterior surface with short, simple hairs beyond setal row. Setae present basal to flabellum at sides, and forming row across base of flabellum on anterior surface, sometimes almost encircling it. Annular hairs tapering or distal ones scarcely lanceolate in Exomalopsis (3.1, Fig. 92A-C), broadly lanceolate in other genera studied (Fig. 92D-J).

In Ancyloscelis (Fig. 92D, E) the flabellum is unusually strongly curved anteriorly at the apex, so that in most views the setal row seems to be near the apex of the flabellum. The short, simple hairs on the anterior side of flabellum are few, minute. Also in this genus, as in many Nomadinae, there is a lamella perhaps made of fused hairs on either side of and closing over the glossal groove (3.2).

Species studied: Ancyloscelis apiformis (SEM), panamensis (C); Caenonomada bruneri (C, SEM); Exomalopsis solani (SEM), zexmeniae (C, SEM); Paratetrapedia lugubris (SEM); Tapinotaspis caerulea (C, SEM); Trigonopedia sp. (C).

Tribe Tetrapediini. Similar to Exomalopsini but seriate hairs relatively long; no noticeable hairs on disannular surface except seriate hairs. Flabellum (7.19) elongate, thick, not or scarcely curved anteriorly, no setae at base or a lateral seta near base but distal end with several setae, variable in length (Fig. 93D), forming a row across apex of flabellum (Fig. 93E, F); anterior surface with short hairs. Annular hairs mostly tapering but distal ones on both surfaces or on posterior surface only broad and commonly three or four dentate at apices (Fig. 93D-F).

Species studied: Tetrapedia sp. (C, SEM), sp. (SEM).

Tribe Melitomini. Glossal rod flat in cross-section or evenly concave on anterior surface (Fig. 66), rather broad; seriate lines on ridges arising lateral to rod; seriate hairs small to minute; disannulate surface otherwise probably without hairs. Flabellum placoid (Fig. 93B, C), glossa scarcely constricted at base of flabellum but narrower than apical part of flabellum, apex strongly curved anteriorly, subtruncate, posterior surface smooth or in Melitoma coarsely transversely wrinkled, anterior surface strongly concave with short simple hairs in space beyond setae; setae forming transverse row across anterior surface of base of flabellum, others scattered at sides of apical part of glossa. Annular hairs frequently broad lanceolate or foliose, some or all along anterior surface in Diadasia and Melitoma foliose with three or four apical points. Annuli, especially in Melitoma, well separated, perhaps because of glossal elongation characteristic of this genus.

Species studied: Diadasia afflicta (C), australis (SEM); Melitoma euglossoides (C), taurea (SEM); Ptilothrix bombiformis (SEM).

Tribe Eucerini. Glossal rod lenticular to semicircular in cross-section (Figs. 69, 70); seriate lines weak ridges, usually close to rod but widely separated from it in Xenoglossa; seriate hairs small to minute; disannulate surface lateral to seriate lines with few (Svastra) to many (Xenoglossa) small hairs (5.11), such hairs probably absent in Melissodes, etc. Flabellum (7.14, Fig. 94A-F) broader than long to elongate oval, glossa not constricted at base of flabellum but narrower than flabellum, apex of flabellum curved anteriorly, rounded or subtruncate apically, posterior surface coarsely cobblestoned; anterior surface

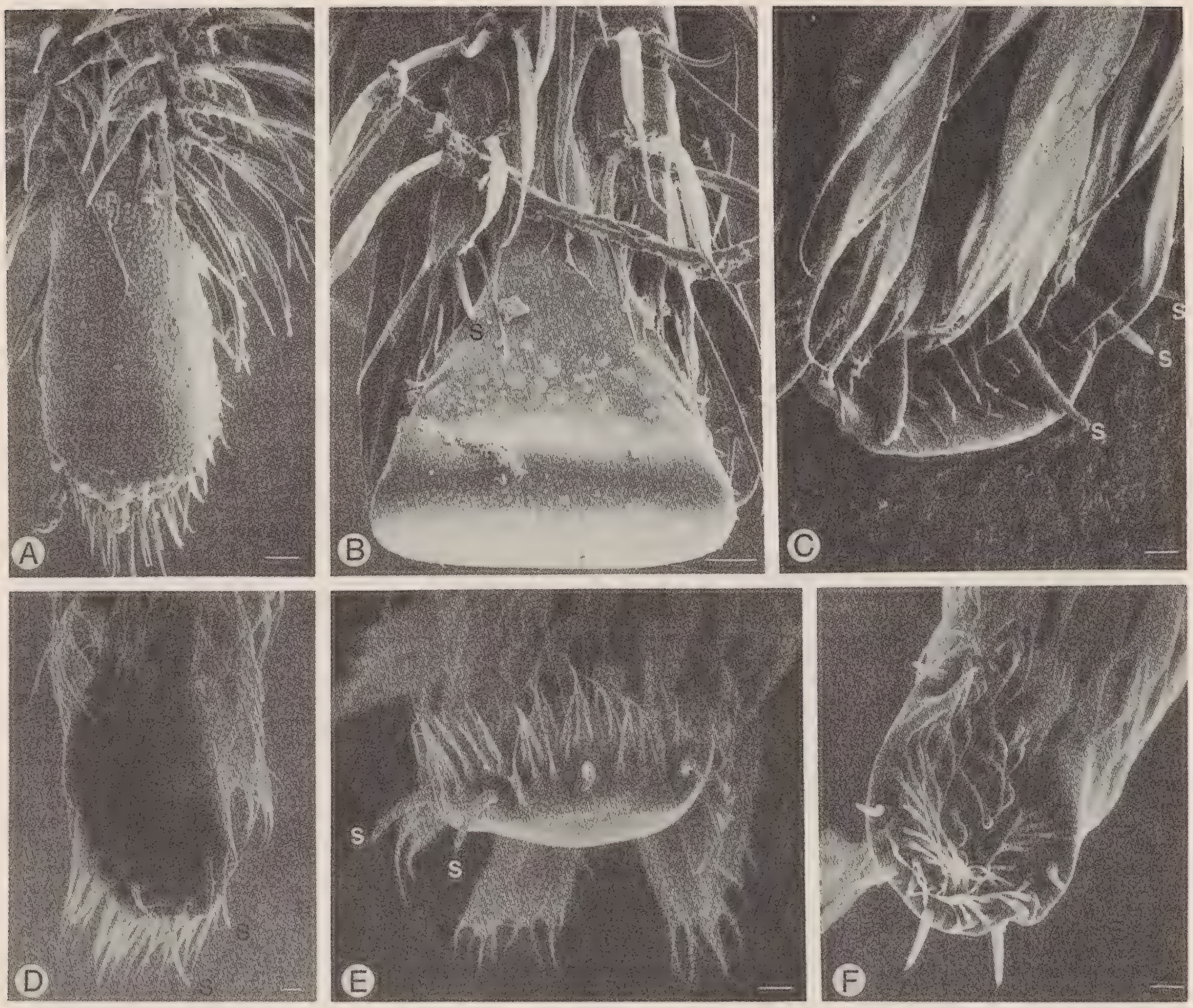


Figure 93. Apices of glossae of Tetrapediini and Melitomini (Anthophoridae). Scale lines represent .01 mm; S = seta. A, Tetrapedia sp., posterior view. B, Diadasia australis, posterior view. C, Melitoma taurea, anterior view. D, E, F, Tetrapedia sp., posterior, apical, and anterior views.

concave with short to rather long simple hairs all or mostly distal to setae; some of these hairs at apex of flabellum usually branched, forming transverse series of small branched hairs (Fig. 94C, D), but these hairs simple in Gaesischia, Alloscirtetica, Xenoglossa, etc. Setae scattered along sides of apical part of glossa; one to four similar setae on each side of anterior surface of flabellum, more distal ones sometimes beyond middle of flabellum; in Xenoglossa setae numerous and forming U-shaped row around sides and apex of flabellum just basal to apical series of hairs; in other genera setae not arranged in row across flabellum. Annular hairs often mostly tapering or very narrowly lanceolate, broadly lanceolate on distal part of glossa, on Xenoglossa broadly lanceolate hairs extending nearly to base.

Species studied: Alloscirtetica tristrigata (SEM); Eucera chrysopyga (C); Florilegus condignus (SEM); Gaesischia exul (SEM); Martinapis luteicornis (SEM); Melissodes agilis (C), lupina (SEM);

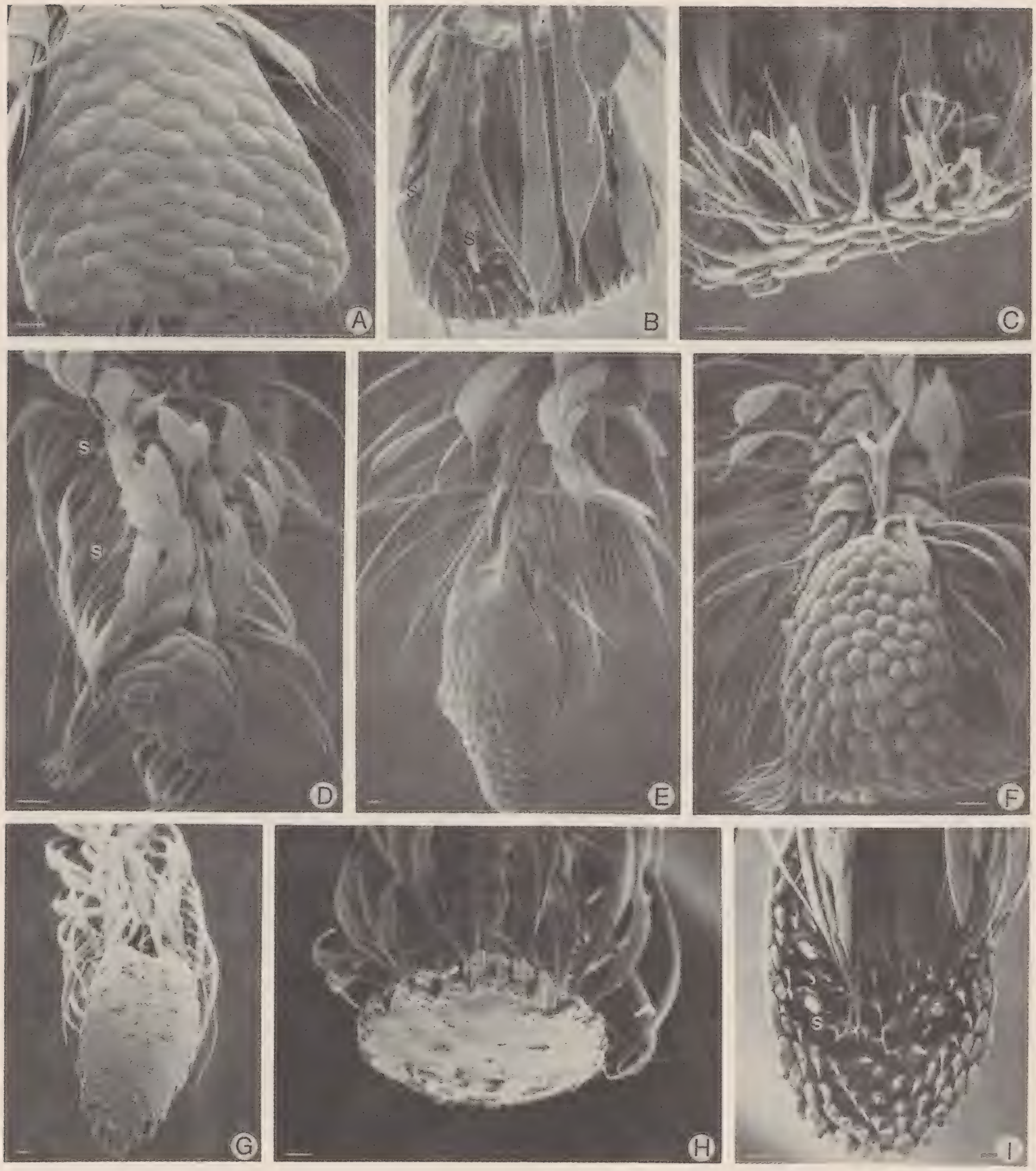


Figure 94. Apices of glossae of Eucerini and Canephorulini (Anthophoridae). Scale lines represent .01 mm; S = seta. A, B, Peponapis pruinosa, posterior and anterior views. C, Svastra obliqua, anterior view of extreme apex; does not show concave anterior surface of flabellum. D, Melissoptila (Ptilomelissa) sp., posterior view. E, Thygater analis, posterior view. F, Svastra obliqua, posterior view. G, H, I, Canephorula apiformis, posterior, anterior with apex of flabellum toward observer, and anterior.

Melissoptila (Ptilomelissa) sp. (SEM); Peponapis crassidentata (C), pruinosa (SEM); Svastra atripes (C), obliqua (SEM); Synhalonia hamata

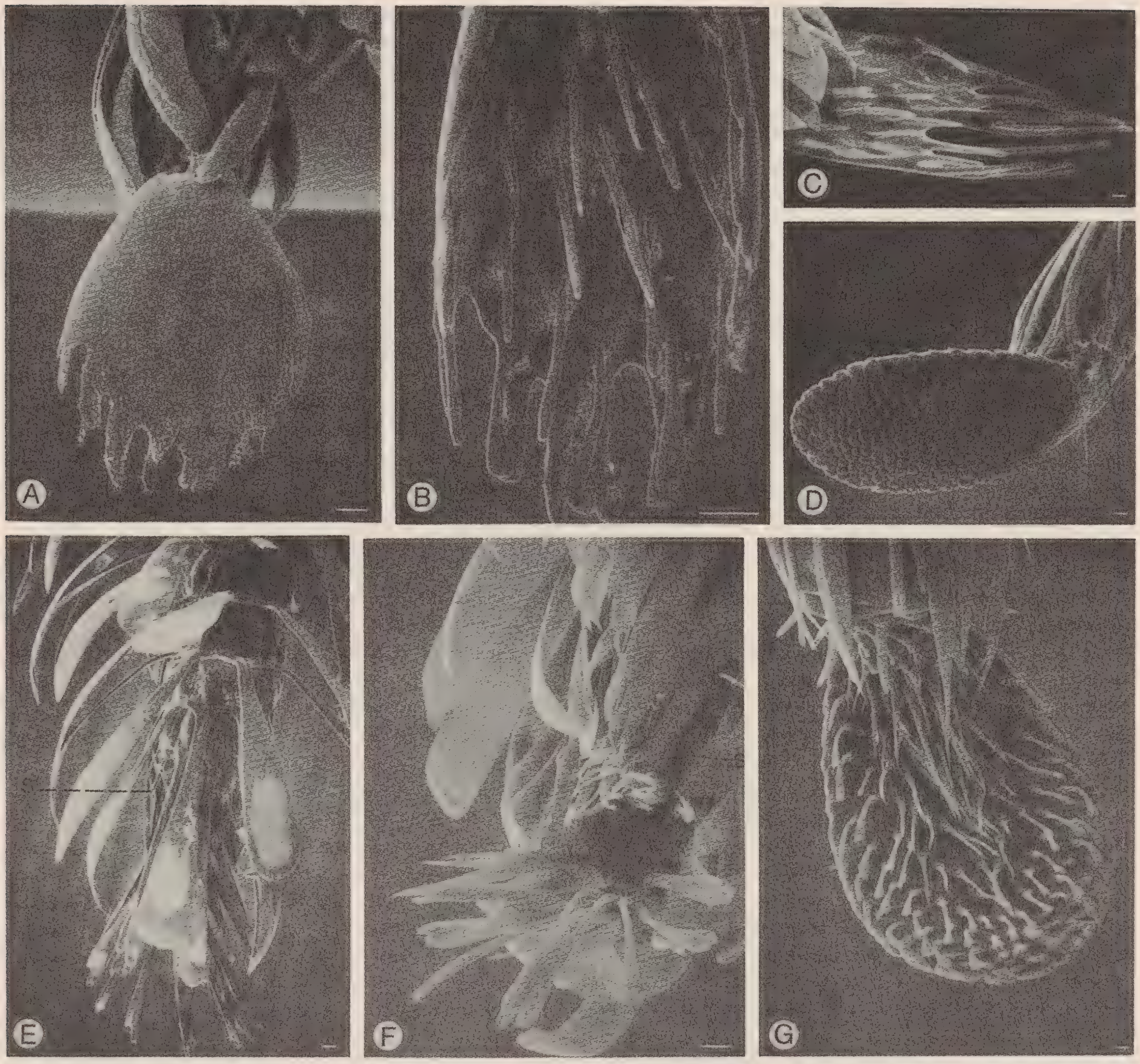


Figure 95. Apices of glossae of Anthophorini. Scale lines represent .01 mm; S = seta. A, B, Anthophora cockerelli, posterior and anterior views. C, Anthophora walshii, anterior view. D, Deltoptila n. sp., posterolateral view. E, Emphoropsis miserabilis, anterior view. F, Emphoropsis pallida, posteroapical view. G, Deltoptila n. sp, anterior view.

(SEM); Thygater analis (C, SEM); Xenoglossa strenua (SEM), fulva (C).

Tribe Canephorulini. Glossal rod rhomboid in cross-section (Fig. 71); seriate hairs abundant, covering low membranous ridges immediately lateral to rod; disannulate surface lateral to seriate lines apparently hairless. Flabellum (7.13, Fig. 94G-I) elongate oval, glossa constricted at base of flabellum, apex of flabellum curved anteriorly, generally rounded but margin with several small lobes from beneath which project several small, flattened, blunt hairs, base of flabellum arched posteriorly; posterior surface of flabellum smooth, anterior surface concave with numerous short hairs which have large bases but taper abruptly to short attenuate apices, these hairs laterally and distally

are blunt and merge with blunt hairs projecting from beneath apical flabellar lobes. Setae absent at or near base of flabellum, not forming transverse row; about three setae on each side of anterior surface of flabellum among small hairs, distal setae beyond middle of flabellum; a few setae scattered among annular hairs of distal part of glossa. Annular hairs partly tapering but those of distal part of glossa mostly lanceolate, the lateral ones broad.

The glossal characters reinforce the distinctness of the Canephorulini from the Eucerini.

Species studied: Canephorula apiformis (C, SEM).

Tribe Anthophorini. Glossal rod rather weak, flat to shallowly U-shaped in cross-section (Fig. 72); seriate lines weak ridges near rod; seriate hairs rather long, at least in Anthophora and Amegilla arising from broad, scale-like bases. Ends of annuli nearly reaching margins of glossal groove which bear dense marginal hairs, some of which at apex of glossa are branched in Anthophora occidentalis. Small scattered hairs on disannular surface between marginal and seriate lines (5.11), in Emphoropsis such hairs near seriate lines arising from incomplete flat scales, one hair per scale. Setae scattered along distal half or third of glossa, on posterior lateral surfaces, not forming row across base of flabellum (7.18). Annular hairs lanceolate, the more distal ones broader and leaf-like except in Deltoptila. Distal specialization highly variable, as follows:

In Anthophora (including Micranthophora), Clisodon, Amegilla, and their relatives, flabellum (7.18) distinct, thin, strongly constricted and arched posteriorly at base, posterior surface smooth, apical margin rounded (Clisodon and some Anthophora) or with one to several deep sinuses separating apical projections (Fig 95A-C); anterior surface concave, with scattered small, simple hairs of variable lengths.

In Emphoropsis and Habropoda, flabellum absent (6.10, Fig. 95E, F); glossa with apical part (last four or five annuli) narrowed to bluntly pointed apex, posterior surface of this region flat and bare. Annular hairs before apical, narrowed part of glossa unusually large, broadly lanceolate or foliose, often hiding glossal apex; annular hairs of narrowed distal part of glossa smaller, especially distally, those of more apical annuli expanded apically and truncate, several of most distal ones arising from extreme apex of glossa.

In Deltoptila, flabellum distinct (7.14, Fig. 95D, G), elongate oval, strongly constricted and arched posteriorly at base, posterior surface with cobblestone pattern; apical margin rounded; anterior surface gently concave with numerous small, unbranched hairs, the distal and marginal ones expanded apically and through shortening, merging into cobblestone pattern of posterior surface.

Species studied: Amegilla comberi (C, SEM); Anthophora cockerelli (C, SEM), occidentalis (C), urbana (SEM), walshii (SEM); Clisodon terminalis (SEM); Deltoptila n. sp. (SEM); Emphoropsis miserabilis (SEM), pallida (SEM); Habropoda deiopea (SEM).

Tribe Melectini. Disannulate surface not invaginated (Fig. 73). Glossal rod weak, flat, scarcely sclerotized. Seriate lines and hairs absent. Ends of annuli not reaching margins of glossal groove which are not to sparsely haired except near apex of glossa where marginal hairs are present and in Xeromelecta lanceolate; disannular surface hairless.

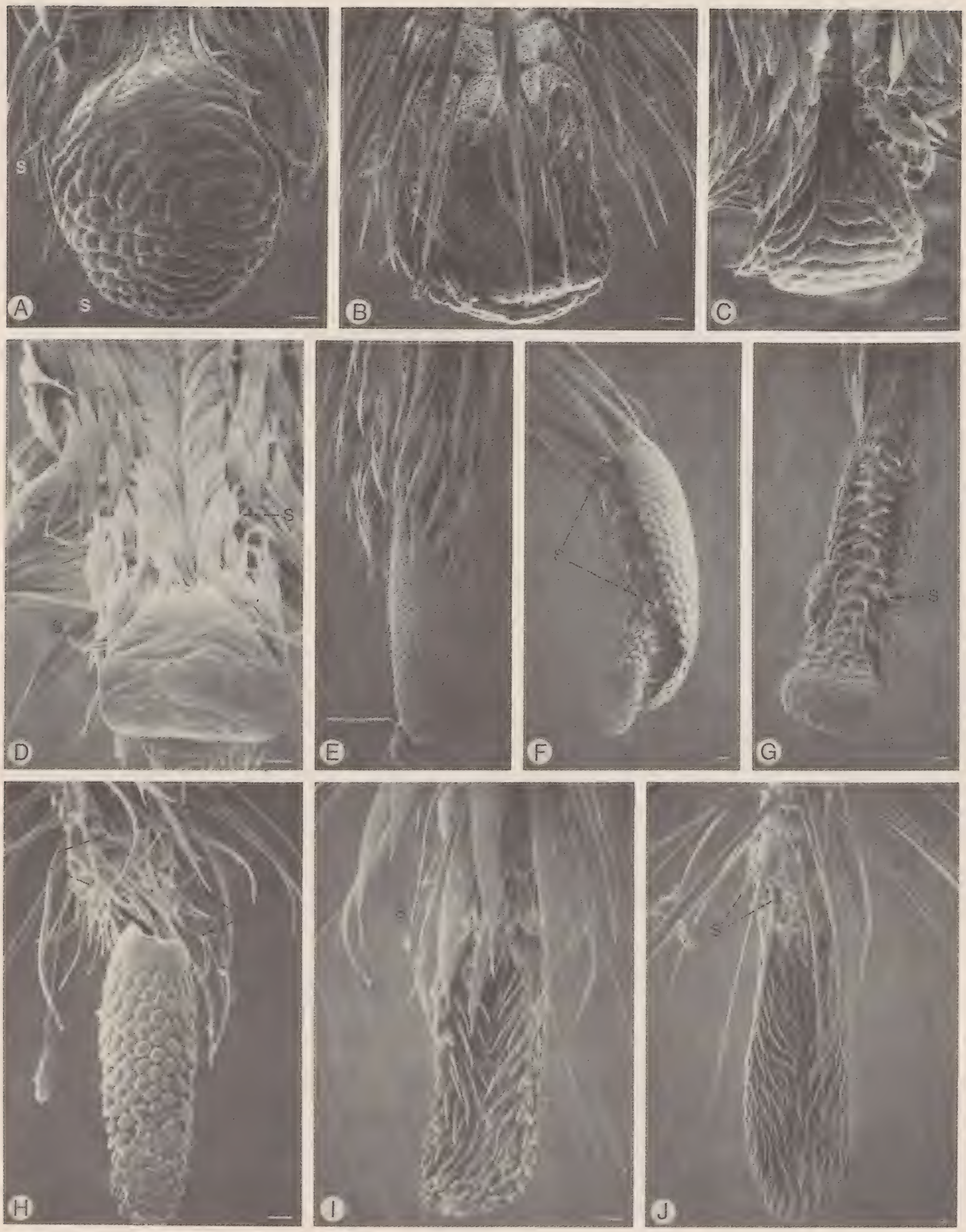


Figure 96. Apices of glossae of Melectini, Ctenioschelini, and Centridini (Anthophoridae). Scale lines represent .01 mm (0.1 mm for E); S = seta. A, B, Melecta armata, posterior and anterior views. C, Thyreus ramosus, posterior view. D, Xeromelecta californica, posterior

Flabellum (7.15, Fig. 96A-D) thin, curved anteriorly, narrowed basally, posterior surface strongly cobblestoned (Melecta), less strongly so (Thyreus), or merely coarsely transversely wrinkled (Xeromelecta), apex rounded or subtruncate; anterior surface with small simple hairs. Setae scattered among annular hairs near sides of distal part of glossa; similar setae forming transverse row or arc across anterior side of flabellum rather near its apex, this row extending basally on each side so that bases of one or more setae are visible in posterior view near flabellar base. Glossal surface distally, minutely granular or papillate. Annular hairs largely tapering but slender-lanceolate on apical part of glossa.

Species studied: Melecta armata (SEM); Thyreus ramosus (C, SEM); Xeromelecta californica (C, SEM).

Tribe Ctenioschelini. Glossal rod lenticular in cross-section (Fig. 74). Seriate lines distinct, well separated from margins of rod, each bearing a row of seriate hairs. Ends of annuli sometimes not or scarcely reaching margins of glossal groove which is margined with simple hairs, or ends of annuli deeply invaginated into glossal groove which is therefore closed by annular hairs. Disannular surface hairless except for seriate hairs. Flabellum (7.16, Fig. 96E-G) consisting of two parts, an elongate preflabellum with thin, rounded apex curved anteriorly, and a small, shorter, rounded postflabellum arising preapically from anterior surface of the preflabellum; bases of both preflabellum and postflabellum narrowed; preflabellum with posterior and lateral surfaces cobblestoned, anterior surface with numerous curved, simple, small hairs arranged in irregular, transverse rows suggestive of annuli but hairs much smaller than annular hairs; postflabellum cobblestoned on all surfaces. Setae scattered lateral to hairy zone on anterior side of preflabellum, the series continued apically onto posterior surface of postflabellum where they form an arched row near apex; a few setae among annular hairs of distal part of glossa. Annular hairs tapering, or near apex of glossa narrowly lanceolate, more broadly so in Mesoplia.

Species studied: Ericrocis arizonensis (SEM), lata (C); Hopliphora funerea (SEM); Mesocheira bicolor (C, SEM); Mesoplia azurea (SEM).

Tribe Centridini. Glossal rod flat in cross-section (Fig. 75), in Epicharis thickened laterally so that it appears to be a partly double rod (Fig. 76); seriate lines very strong ridges rising from margins of rod and in Epicharis curved toward one another at summits, largely enclosing round bacular canal; seriate hairs of moderate length but mostly fused to form a lamella (5.10) here and there broken into hairs, rising from summit of seriate ridge. (An alternative explanation is that there is a lamella, sometimes torn into hair-like units, in place of seriate hairs.) Disannulate surface lateral to seriate lines with scattered very minute hairs (5.11). Flabellum (7.14, Fig. 96H-J) elongate, flattened, strongly constricted and arched posteriorly at base, posterior surface with cobblestone pattern which is exaggerated at margins which are

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view. E, Hopliphora funerea, posterior view. F, Mesocheira bicolor, lateral view. G, Mesoplia azurea, anterior view; some hairs of the basal half of the surface are broken off. H, I, Centris atripes, posterior and anterior views. J, Epicharis rustica, anterior view.

therefore finely lobed, these lobes grading into small hairs of anterior surface; apex of flabellum weakly curved anteriorly, anterior surface with numerous short simple hairs. Seta present on posterior lateral surfaces of glossa basal to flabellum, one or two on each side among annular hairs, also forming row across anterior surface basal to flabellum. Annular hairs mostly tapering but distal ones often lanceolate.

Species studied: Centris atripes (SEM), poecila (C); Epicharis elegans (C), rustica (SEM).

Subfamily Nomadinae. Disannulate surface not invaginated as in Nomada, to deeply so like that of most long-tongued bees in Thalestria (Figs. 77-81). Glossal rod usually weak, absent or only a feeble dark zone in Nomada, Biastes, etc., but well sclerotized in Caenoprosopis, Isepeolus, and Leiopodus, distinct and V-shaped in cross-section in Thalestria. Seriate lines absent or nearly so, except in Triepeolus and Thalestria which have small ridges adjacent to and on each side of rod. Seriate hairs usually absent or very sparse and minute, but abundant and minute in Triepeolus and Thalestria, absent on distal part of glossa in Triepeolus. Disannulate surface otherwise hairless or with a few minute hairs, more numerous in Triepeolus (5.11). Annular hairs slender and tapering on basal part of glossa, for example in Triepeolus, and Nomada, but apically broadened, lanceolate, often broadly so, in Morgania, Isepeolus, Protepeolus, and Leiopodus many of them with two or three apical points, in Osiris many of those of anterior surface greatly expanded with about five to seven apical points. Hairs(?) on either side of disannular surface often expanded and sometimes fused into a thin broad lamella on each side, this lamella may project away from glossa but usually lies over and completely hides disannular surface (3.2); such structures present in Leiopodus (Figs. 80, 97G), Osiris (Fig. 97G), Nomada (Figs. 79, 98E), Epeoloides (Fig. 97K), Isepeolus, Caenoprosopis, Holcopasites, and Morgania (Fig. 98A), but apparently absent in Biastes, Thalestria, Triepeolus, Epeolus, and Doeringiella.

Distal specialization (Figs. 97, 98) variable, sometimes (e.g., in Nomada, Epeoloides, Ammobatoides, Morgania, Holcopasites, and Caenoprosopis) essentially a placoid flabellum, but with glossa not or scarcely narrowed at its base; flabellum distinctly wider than glossa at flabellar base in Ammobatoides and Holcopasites; posterior surface of flabellum smooth or with weak coarse wrinkles in Epeoloides and Ammobatoides; apical margin of flabellum rounded, curved anteriorly, projecting little beyond transverse row of setae (7.8, 7.9); flabellum without small hairs on the very limited anterior side (except annular hairs, the distal ones of which may arise near base of distal specialization) or in Nomada with a narrow zone of small, simple or lan-

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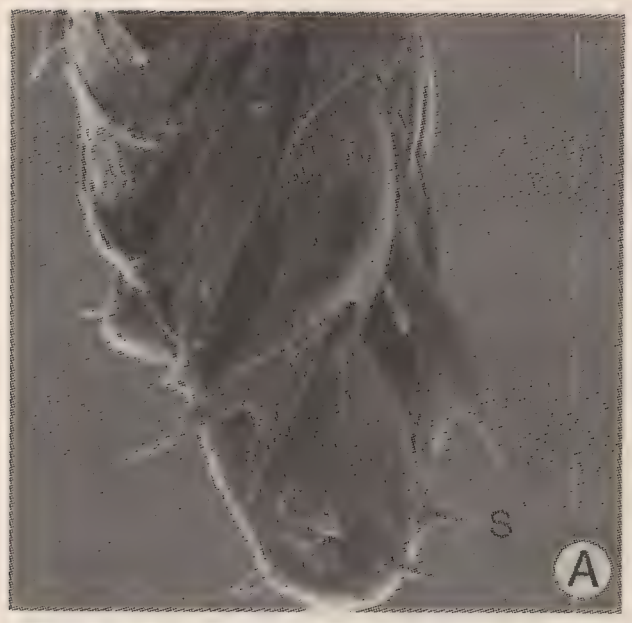
Figure 97. Apices of glossae of Nomadinae (Anthophoridae). Scale lines represent .01 mm; S = seta. A, Isepeolus viperinus, posterior view. B, C, Thalestria spinosa, anterolateral and anteroapical views, posterior surfaces at lower right in both. D, E, Doeringiella bizonata, posterolateral and anterolateral views. F, Triepeolus verbesinae, anterolateral view. G, H, Leiopodus lacertinus, posterior and anterior views. I, J, Osiris sp., posterior and posterolateral apical views. K, L, Epeoloides pilosula, posterior and anterior views. M, Osiris sp., anterolateral view.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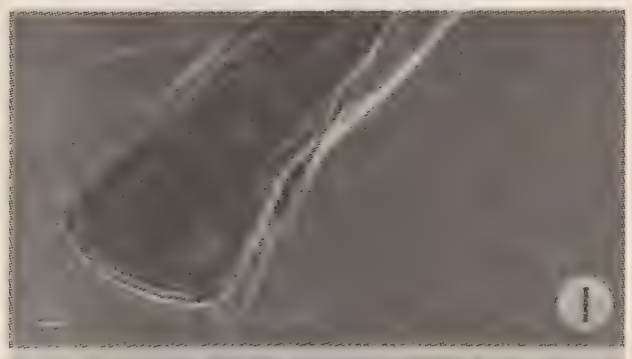
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ceolate hairs arising between row of setae and apical flabellar margin (Fig. 98C). Setae present, one or two at each side of apical part of glossa and transverse row or arch extending across anterior flabellar surface preapically, these setae often quite large and extending beyond flabellar margin (Fig. 98F). Osiris and Leiopodus (Fig. 97G-J, M) are similar but the flabellum is thick, not or little curved anteriorly, transversely wrinkled apically in some Osiris, and the setae are small and widely separated, in Osiris scattered and not in a neat row (7.10).

A few genera have distal specializations similar to those of Holcopasites, etc. (i.e., placoid), but the transverse arch of setae extends basally onto posterior surface, these setae arising along the margins of the flabellum (Biastes, Neolarra, Fig. 98L) or on the basal part of posterior flabellar surface (Pseudodichroa) (7.10, Fig. 98H).

Distal specializations of Isepeolus, Protepeolus, Doeringiella, Epeolus, and Triepeolus are thickened, not placoid, scarcely curved anteriorly, blunt, with a few short setae on both anterior and posterior surfaces (6.9). While the setae are apparently derived from setae of the transverse arch, no such row of setae is recognizable (7.11). In Thalestria the structure is similar but the bare flabellar area on the posterior surface is elongated basad, so that it is elongate oval; many annular hairs are on the corresponding anterior surface (7.1, 7.11).

Species studied: Epeolini. Doeringiella bizonata (SEM); Epeolus pusillus (SEM); Thalestria spinosa (C, SEM); Triepeolus verbesinae (C, SEM). Nomadini. Nomada annulata (C, SEM). Osirini. Osiris obtusus (SEM). Protepeolini. Isepeolus viperinus (C, SEM); Leiopodus lacertinus (C, SEM). Epeoloidini. Epeoloides pilosula (SEM). Ammobatini. Morgania histrio transvaalensis (SEM); Pseudodichroa capensis (SEM). Caenoprosopidini. Caenoprosopis crabronina (C, SEM). Holcopasitini. Holcopasites arizonicus (SEM), heliopsis (C). Biastini. Biastes brevicornis (C, SEM). Ammobatoidini. Ammobatoides abdominalis (SEM). Neolarrini. Neolarra verbesinae (SEM).

Subfamily Xylocopinae. Tribe Ceratinini. The following is based on the nonparasitic Ceratinini; parasitic forms are described later. Glossal rod distinct, crescentic in cross-section (Figs. 84, 85). Seriate lines weak ridges lateral to margins of rod. Seriate hairs small, abundant, in a row. Disannulate surface lateral to seriate lines hairless. Flabellum (Fig. 99D-I) tapering basally to rod, apex rounded or subtruncate, curved anteriorly, posterior surface smooth, anterior surface concave, in allodapine genera extending well beyond arch of setae and with small simple hairs (absent in Macrogalea, few in Exoneurella), in Ceratina, Pithitis, and Manuelia extending not so far beyond arch of setae and with only narrow band of hairs arising in space between setal bases and apex of flabellum (7.8). Setae often recognizable on anterior surface of glossa among annular hairs, basal to flabellum; a transverse arch across anterior surface of flabellum consists of large setae, often only four but six or more in Macrogalea. Annular hairs lanceolate, especially laterally and on distal part of glossa.

Among parasitic genera, Inquilina has a glossa similar to that of other allodapine bees, but Nasutapis and Eucondylops (5.3) have greatly reduced glossae, described as follows: Glossa rather short, in Eucondylops tapering with the apex attenuate as in short-tongued bees.

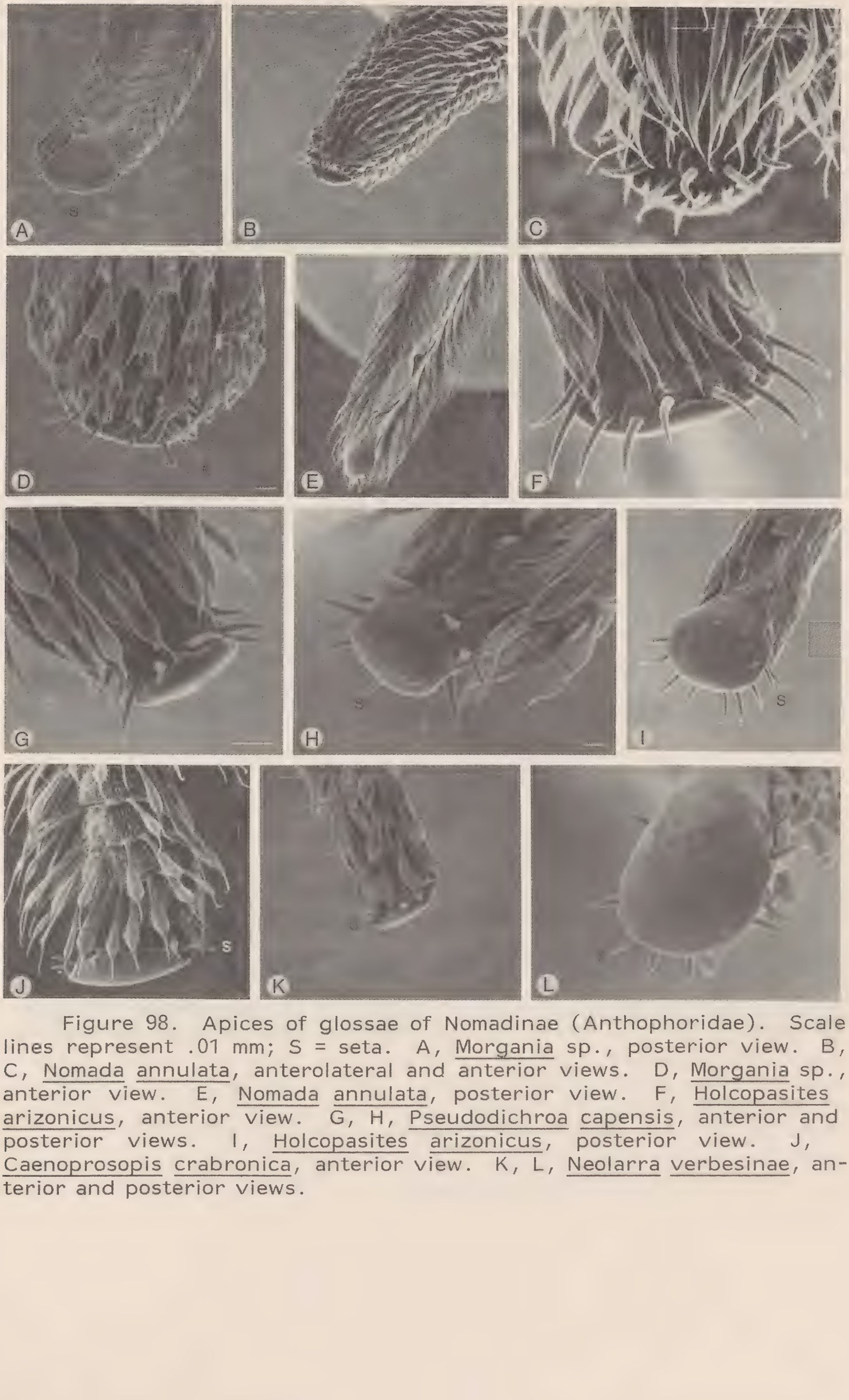


Figure 98. Apices of glossae of Nomadinae (Anthophoridae). Scale lines represent .01 mm; S = seta. A, Morgania sp., posterior view. B, C, Nomada annulata, anterolateral and anterior views. D, Morgania sp., anterior view. E, Nomada annulata, posterior view. F, Holcopasites arizonicus, anterior view. G, H, Pseudodichroa capensis, anterior and posterior views. I, Holcopasites arizonicus, posterior view. J, Caenoprosopis crabronica, anterior view. K, L, Neolarra verbesinae, anterior and posterior views.

Disannular surface exposed, depressed to form a channel in Nasutapis, not depressed in Eucondylops. Glossal rod and seriate lines and hairs absent; disannulate surface with scattered tiny hairs in Nasutapis, which also has moderately dense marginal hairs. Flabellum absent (6.1); glossal apex with long annular hairs like those in more proximal positions (Fig. 100I). Annuli few and widely separated especially in Eucondylops. Setae absent. Annular hairs slender, tapering.

Species studied: Allodape ceratinoides (SEM), stellarum (C); Allodapula dichroa (SEM); Braunsapis calidula (SEM), facialis (C); Ceratina calcarata (C), laeta (C), neomexicana (SEM), rupestris (C), (Ceratinidia) sp. (C); Eucondylops reducta (C, SEM); Exoneura hamulata (SEM); Exoneurella lawsoni (SEM); Halterapis nigrinervis (SEM); Inquilina excavata (SEM); Macrogalea candida (C, SEM); Manuelia gayi (C, SEM); Nasutapis straussorum (C, SEM); Pithitis binghami (C, SEM).

Tribe Xylocopini. Glossal rod shallowly U-shaped in cross-section (Figs. 82, 83); seriate lines on very strong ridges rising from lateral margins of rod and approaching one another at summits, thus largely enclosing bacular canal; seriate hairs numerous but minute, on summits of ridges. Disannulate surface lateral to seriate lines with scattered minute hairs (5.11). Distal annulus far short of base of flabellum, leaving bare shank (7.17) which is abruptly constricted at base of flabellum. Flabellum broadly oval, flat, strongly constricted at base, posterior surface with weak cobblestone pattern, apex rounded and weakly curved anteriorly, anterior surface with numerous, small but moderately long, curved hairs, simple in Xylocopa augusti, with one or two branches each in X. virginica. Transverse row of about eight setae arising from shoulder at distal end of shank; no setae on flabellum, no setae recognizable among annular hairs. Annular hairs tapering.

Several of the main features were also illustrated for X. capitata by Louw and Nicholson (1983).

Species studied: Lestis aeratus (C); Xylocopa augusti (SEM), varipuncta (C), virginica (C).

FAMILY APIDAE
(Figs. 86-91, 100A-H, 101)

Members of this family share the characters listed above for long-tongued bees. The glossa of the Apidae is quite variable; for that reason and because of the enormous variability in anthophorid glossae, there are no diagnostic glossal features of the Apidae. However, the glossal rod is usually thicker than in anthophorids and has two or even three longitudinal darkened lines, so that it appears double or triple. Such rods are uncommon in Anthophoridae.

Subfamily Bombinae. Tribe Euglossini. Glossa flattened, three to six times as wide as thick (Figs. 86, 87). Glossal rod (4.5) consisting of two thickenings in floor or sides of glossal canal, often with a weak thickening (reduced distally) between the two, so that there appear to be two or three closely parallel rods; glossal canal small. Seriate lines just lateral to lateral rods, and bearing minute seriate hairs

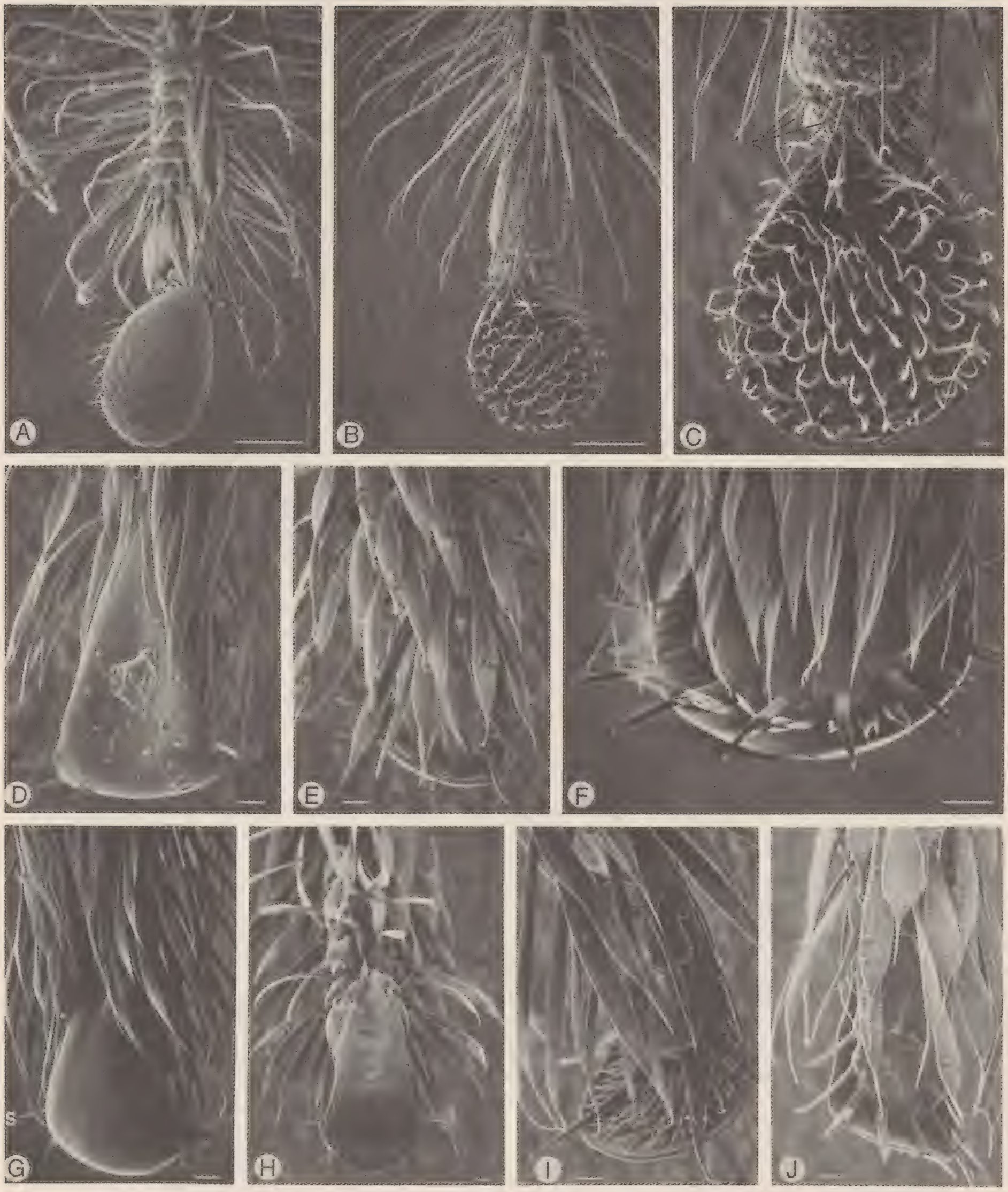


Figure 99. Apices of glossae of Xylocopinae (Anthophoridae). Scale line represents .01 mm (0.1 mm for A and B); S = seta. A, B, C, Xylocopa augusti, posterolateral, anterior, and anterior views. D, E, Ceratina neomexicana, posterior and anterior views. F, G, Manuelia gayi, anterior and posterior views. H, I, Allodape ceratinoides, posterior and anterior views. J, Macrogalea candida, anterior view.

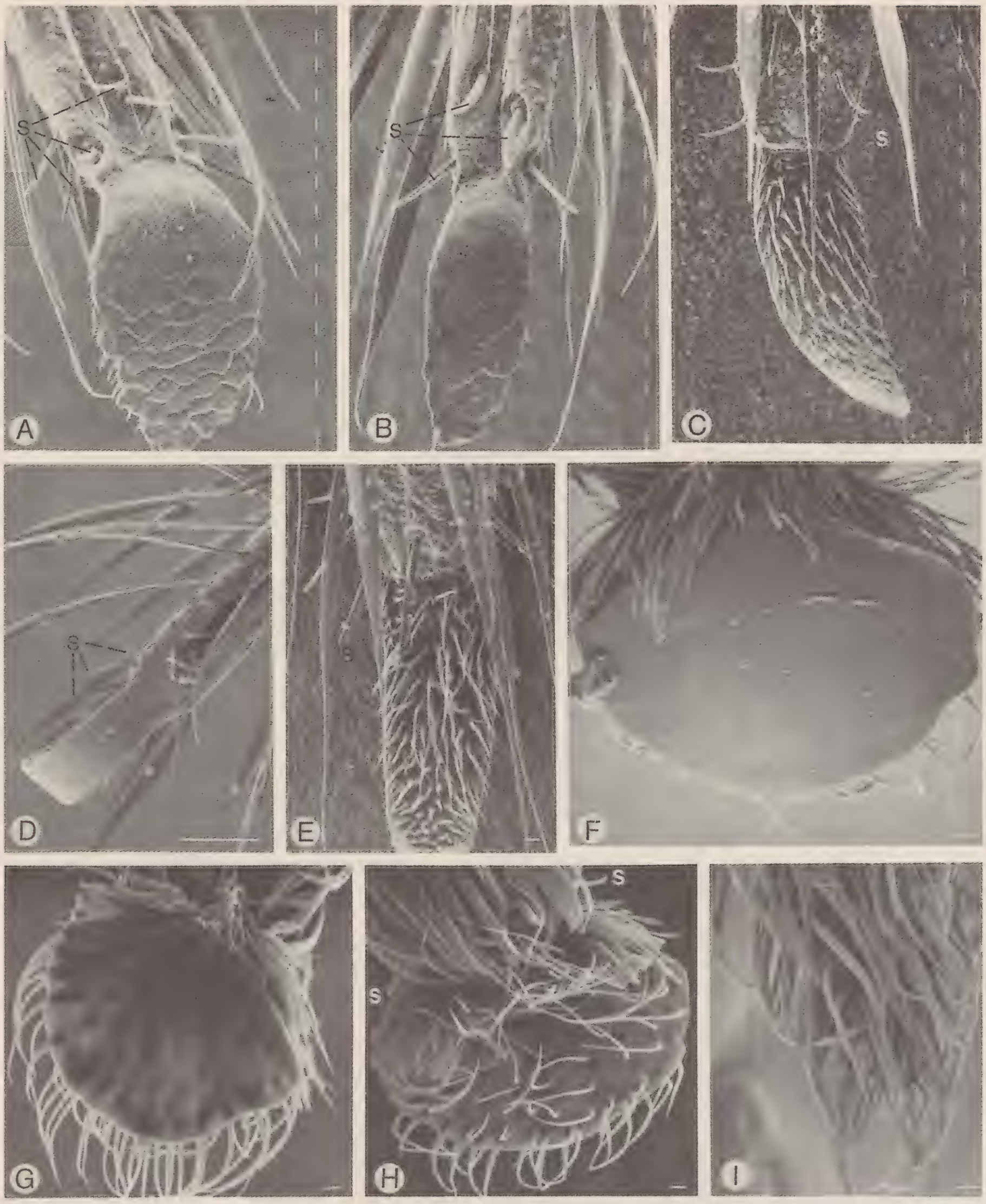


Figure 100. Apices of glossae of Euglossini, Bombini (Apidae), and Xylocopinae (Anthophoridae). Scale lines represent .01 mm (0.1 mm for D); S = seta. A, Eufriesea surinamensis, posterior view. B, Eufriesea sp., posterior view. C, Eufriesea surinamensis, anterior view. D, E, Eulaema meriana, posterior and anterior views. F, G, H, Bombus morrisoni, posterior, posterior, and anterior views. I, Nasutapis straussorum, posterior view.

distally (in at least Eulaema). Disannulate surface otherwise hairless. Marginal hairs sparse and short. Distal annulus far short of base of

flabellum, leaving bare shank (7.17) which is constricted before base of flabellum. Flabellum several times as long as wide, flat, strongly constricted at base, posterior surface with weak cobblestone pattern, apex narrowly rounded and moderately to strongly curved anteriorly, anterior surface with numerous small hairs (Fig. 100A-E). Several setae scattered on anterior surface of shank and near apex of shank on posterior surface; no setae on flabellum, none seen among annular hairs. Annular hairs (3.3) reduced or absent on much of anterior surface; enormous and broadly lanceolate along lateral margins, these large hairs partly closing over channel along concave posterior surface of glossa; almost no hairs between these large hairs and glossal groove, although this zone is crossed by weak extensions of annuli.

A possible alternative explanation of the glossal structure of Euglossini is that the disannulate surface is broadly exposed, the weak, hairless annuli across it being secondary thickenings, and the largely enclosed tube being the bacular canal rather than the glossal canal. This explanation seems unlikely in view of the condition in related bees and the presence of what appear to be marginal hairs along the margins of the glossal groove. However, the glossal canal is singularly small, intermediate in size between what one would expect for a glossal canal and for a bacular canal, and its floor and walls are extensively sclerotized by parts of the rod; in this respect it suggests a bacular canal.

Species studied: Eufriesea surinamensis (SEM), violacea (C), sp. (C); Euglossa chalybeata (SEM), cordata (C); Eulaema cingulata (C), meriana (SEM); Exaerete smaragdina (C).

The distinctive glossa of the Euglossini does not support placement of this tribe in the same subfamily as the Bombini. The possibility of such a relationship exists, however; the familiar euglossine features are synapomorphies of members of that tribe and do not establish any other relationship.

Tribe Bombini. Glossal rod nearly flat in cross-section, darkened on both sides of midline so that it appears double, a broad, thick prismatic strip (in which the dark bands lie) on floor of glossal canal, the whole probably functioning as a large rod (Figs. 90, 91). Seriate lines in form of strong ridge on each side of rod; seriate hairs numerous, small. Disannulate surface lateral to seriate lines with numerous minute hairs (5.11). Distal annulus far short of base of flabellum, leaving bare shank (7.17) which is constricted just before base of flabellum; flabellum (7.12) broader than long, flat, placoid (Fig. 99F-H), apex rounded (slightly lobed), curved anteriorly, posterior surface smooth, anterior surface with numerous small hairs, mostly simple but largest ones with one or two branches, these hairs densest toward flabellar base which they surround and cover (Fig. 99F). Setae forming row (partly hidden among short hairs) across apex of shank on anterior side; a few small setae on anterior surface of shank; scattered setae among annular hairs near sides of posterior surface of distal part of glossa. Annular hairs slender, tapering.

Species studied: Bombus pennsylvanicus (C), morrisoni (SEM); Psithyrus variabilis (C).

Subfamilies Meliponinae and Apinae. Glossal rod darkened on both sides of midline (clear in Apis) so that in Meliponinae it appears

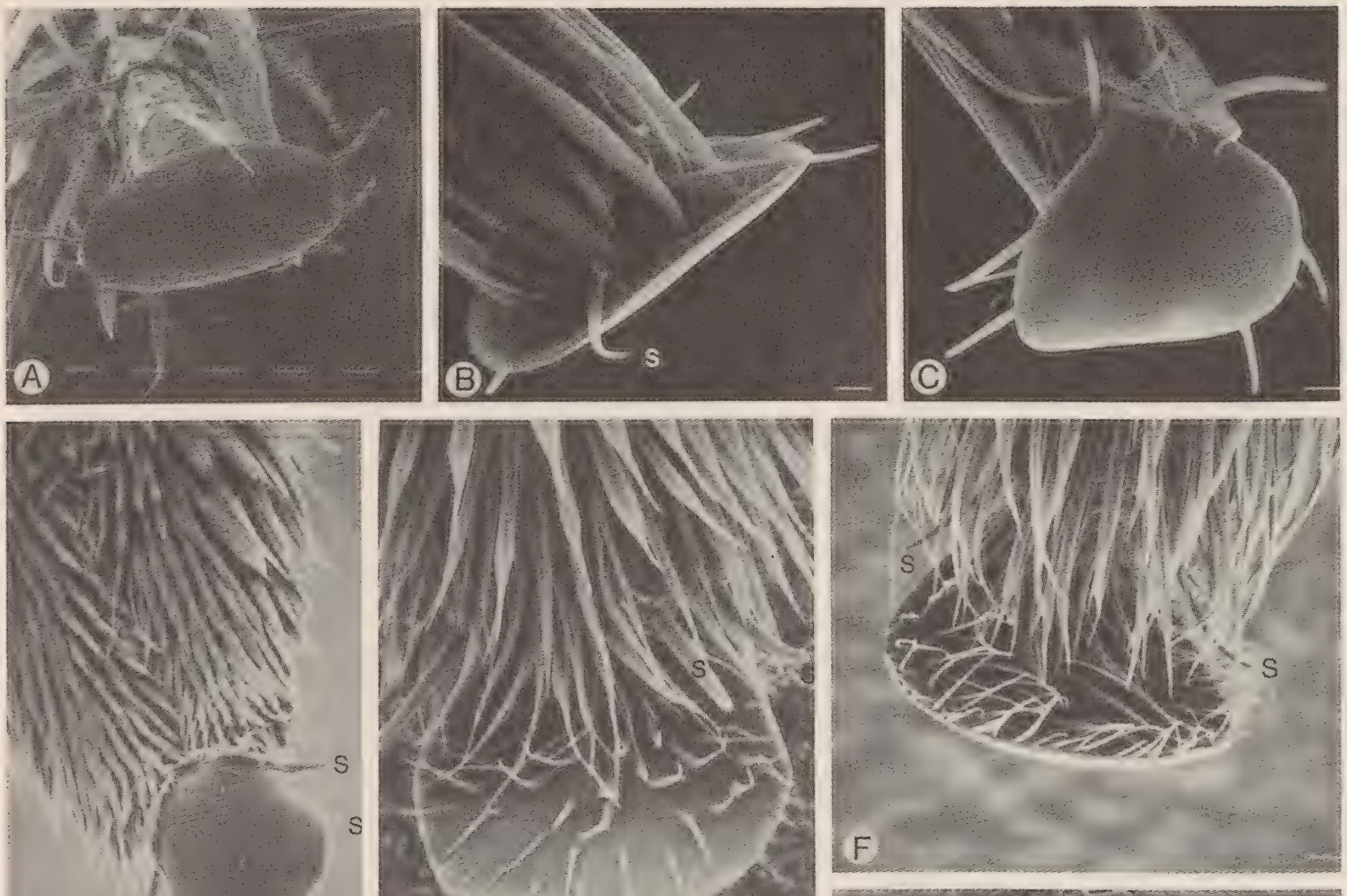


Figure 101. Apices of glossae of Meliponinae and Apinae (Apidae). Scale lines represent .01 mm; S = seta. A, B, C, Trigona (Partamona) musarum, anterior, anterior, and posterior views. D, E, Dactylurina staudingeri, posterior and anterior views. F, Meliponula bocandei, anterior view. G, Apis mellifera, posterior view. H, Lestrimelitta limao, anterior view with flabellum curved forward to show posterior surface. I, J, Apis mellifera, posterior and anterior views.

double, rod itself much larger than dark areas, prismatic, and nearly surrounding round bacular canal (Figs. 88, 89). Seriate lines on summits of lateral extensions of rod that enclose bacular canal; seriate hairs numerous, small, directed mesad and closing over bacular canal.

Disannulate surface lateral to seriate lines with numerous minute hairs (5.11) in some areas, sometimes minutely papillate. Flabellum (7.12, Fig. 101) as broad as or broader than long (longer than broad in male Apis), flat, placoid, apex rounded (slightly lobed in Lestrimelitta and Apis), curved anteriorly, posterior surface smooth, anterior surface with numerous (few in Lestrimelitta and male Apis), small, simple hairs (branched near margin in worker Apis), densest toward flabellar base and often spreading as a narrow collar around base of flabellum, distal to annular hairs. Setae two or four (more in Apis), in transverse row just basal to flabellum on anterior side, none on flabellum; scattered setae among annular hairs on posterior surface of distal part of glossa. Annular hairs tapering to slender lanceolate.

The similarities of glossal structures of Meliponinae, Bombini, and Apinae are impressive. They do not support the isolated position given the Meliponinae by Winston and Michener (1977).

Species studied: Apinae. Apis dorsata (C), florea (C), mellifera (C, SEM). Meliponinae. Dactylurina staudingeri (C, SEM); Lestrimelitta limao (C, SEM); Melipona fasciata (C), marginata (C), rufiventris brachychaeta (C, SEM); Meliponula bocandei (C, SEM); Trigona buyssoni (C), capitata zexmeniae (C), chanchamayoensis (C), frontalis (C), musarum (SEM), schrottkyi (C), (Hypotrigona) sp. (C), (Plebeia) sp. (C).

DISCUSSION

The glossal structure provides a wealth of morphological details which are of significance in understanding the systematics and evolution of the bees. The major division of the bees into short-tongued and long-tongued families (Michener and Greenberg, 1980) is in general supported. Rather curiously, tongue length is not reliable in support of this distinction. The following glossal characters are of interest in this connection:

(1) The short-tongued families have the disannular (morphologically posterior) surface of the glossa exposed (rarely invaginated, as in Melitturga, Fig. 50) and not or only feebly strengthened by a glossal rod. Because of the exposed disannulate surface the annuli do not go all the way around the glossa. In long-tongued families, however, the disannulate surface is invaginated along with the glossal rod (which is a median thickening of this surface); the annuli therefore seem to go most of the way around the glossa. Sometimes the surface and rod are everted and exposed in dead specimens. In some parasitic genera the invagination and rod have been lost; incomplete invagination in specimens of Fideliidae and Tapinotaspis (Figs. 62 and 70) could represent retention of a primitive feature but we suspect it is merely a result of partial eversion.

(2) When present, the seriate hairs of short-tongued bees are divergent and the hairs themselves commonly large and some of them branched. [Recognizable seriate hairs are absent in Colletidae and Stenotritidae, hairs being widely scattered over the disannulate surface of the glossa; in some members of other families the seriate hairs have been nearly or entirely lost (Figs. 28, 47).] In contrast, the seriate hairs of long-tongued bees, when present as they usually are, are convergent, small to minute, simple, and arise from a ridge along each

edge of or near the glossal rod. The Ctenoplectridae, a family of short-tongued bees with many features of long-tongued bees, has convergent seriate hairs like long-tongued bees (Fig. 58).

(3) Short-tongued bees usually have an apically attenuate glossa (i.e., with the lateral apical margins concave due to the apex being drawn out), with the annulate and disannulate surfaces both reaching the apex, the former bearing annular hairs, the latter seriate hairs. In the Colletidae (except certain males) the disannulate surface is expanded beyond the morphological apex of the glossa to form the glossal lobes (Fig. 1). In most long-tongued bees the disannulate surface is expanded beyond the morphological apex of the glossa to form the flabellum. Both flabella and the colletid glossal lobes have disannulate hairs on their anterior surfaces, suggesting similar origins for these structures. Elsewhere the disannulate surface is entirely posterior (or invaginated).

Further consideration of flabella is necessary, however, for they are neither restricted to long-tongued bees nor characteristic of all such bees. No bee with a really short glossa has a flabellum or any similar distal specialization. A few unrelated groups of short-tongued bees with rather long glossae have distal specializations suggestive of flabella, or have true flabella, sometimes much like those of long-tongued bees. Thus while short-tongued bees with rather long glossae and no flabella (Fig. 26) do exist, as well as long-tongued bees without flabella, there is a tendency for an association between glossal length and presence of a flabellum.

Various steps in flabellar development among short-tongued bees are described in the Comparative Account, paragraphs 6.5-6.8 and 7.2-7.6. This is not a phylogenetic series. Some species of Panurginae (Andrenidae), Dufoureinae (Halictidae), and all Ctenoplectridae are involved, with an interesting broadened glossal apex also in Dasypoda (Melittidae). In the Panurginae every gradation exists from no suggestion of a flabellum (Fig. 51A-C) to a well formed flabellum (Fig. 51F-J) to a flabellum incredibly like that of long-tongued bees (Fig. 52A-E, Perdita and Callonychium). The similarity between the placoid flabellum of Perdita or Callonychium and that of long-tongued bees involves not only position, but also shape, the smooth, convex, posterior surface, the forward curvature, the curved row of setae across the base of the anterior surface, and the small disannular hairs on the anterior surface distal to the setal row. It is hard to suppose that the development of such similar and complex placoid flabella could be independent in Panurginae and long-tongued bees. Yet Panurginae have so many common derived features (e.g., lack of the gonobase, two subantennal sutures) not shared with long-tongued bees that it hardly seems believable that long-tongued bees and the small group of Panurginae having flabella are sister groups. The remarkable flabellar similarities must have arisen from convergence, along with some elongation of the basal segments of the labial palpi, a feature of many Panurginae that is more fully developed in long-tongued bees.

Flabella are lost in certain groups that normally have them. The flabellum was quite probably lost in ancestors of Perdita texana although that species could represent an ancestral preflabellar condition. The flabellum was certainly lost in the Habropoda-Emphoropsis group of

Anthophorini; other members of this tribe and all related tribes possess flabella. Numerous stages of flabellar reduction can be found in the parasitic anthophorid subfamily Nomadinae (see Comparative Account, paragraphs 7.9-7.11). These do not form any single series; reduction must have occurred independently in different nomadine phyletic lines. Loss of flabella also occurred in the parasitic allodapine xylocopines, Eucondylops (derived from the nonparasitic genus Allodapula which has a flabellum) and Nasutapis (derived from the nonparasitic genus Braunsapis which has a flabellum) (Michener, 1970).

Various Nomadinae as well as Eucondylops and Nasutapis not only show reduction or loss of flabella, but also reduction or loss of the glossal rod and the glossal canal, so that the disannulate surface is no longer invaginated (Figs. 78-81). Another parasitic group, the Melectinae, while having a flabellum, shows similar reduction of the glossal rod and canal (Fig. 73). Although some parasitic groups retain glossal structure normal for their families or subfamilies, the reduction in glossal complexity in several parasitic groups suggests that much of the glossal complexity may involve adaptations for nest construction or provisioning rather than merely for feeding. Parasitic bees presumably feed like any other bees. (Nasutapis and Eucondylops are not known to go to flowers, but the other groups mentioned visit flowers freely to take nectar.) They do not, however, have to construct and provision nests, as do females of nonparasitic forms. Glossae are known to be involved in waxing or varnishing cells and the like, and it is likely that some of their features are correlates of such behavior.

One would expect the glossa to be well equipped with organs of taste and or tactile sensilla. This may be so, but the only structures that we have identified as presumably sensory are the setae, which are small and sparse. In many sphecoid wasps setae form an apical row across the distal glossal margin. In Colletidae they commonly form a preapical row on the anterior surface (Fig. 1). They are usually absent, however, in short-tongued bees, but occur in the following: many Colletidae (anterior surface, also posterior surface in Diphaglossinae), Stenotritidae (anterior and posterior surfaces), Halictidae (only seen among annular hairs of Rophites), Andrenidae (only seen near glossal apices of a few genera of Panurginae), Oxaeidae (among extremities of annuli in middle and basal parts of glossa), Melittidae (among annular hairs of Macropis only), and Ctenoplectridae (near flabellum and on its anterior surface). Among long-tongued bees, setae are usually present among annular hairs and especially at the base of or on the flabellum. The descriptions and illustrations of taxa give more detailed accounts of the locations of setae. Since setae are sometimes hard to find among the much longer and usually broader annulate hairs, we may have missed them in some forms that possess them.

In order to provide a visually helpful summary of part of our data, we have made a cladistic analysis using the Wagner 78 computer program of S. J. Farris as implemented on the University of Kansas academic computer. Table 1 lists the synapomorphies which we have recognized with the corresponding plesiomorphies in parentheses, and in most cases a brief indication of the reason for our decision as to the polarity of each variable. The taxa are at the tribal level and above. The data come only from the species listed earlier in this paper; the use of

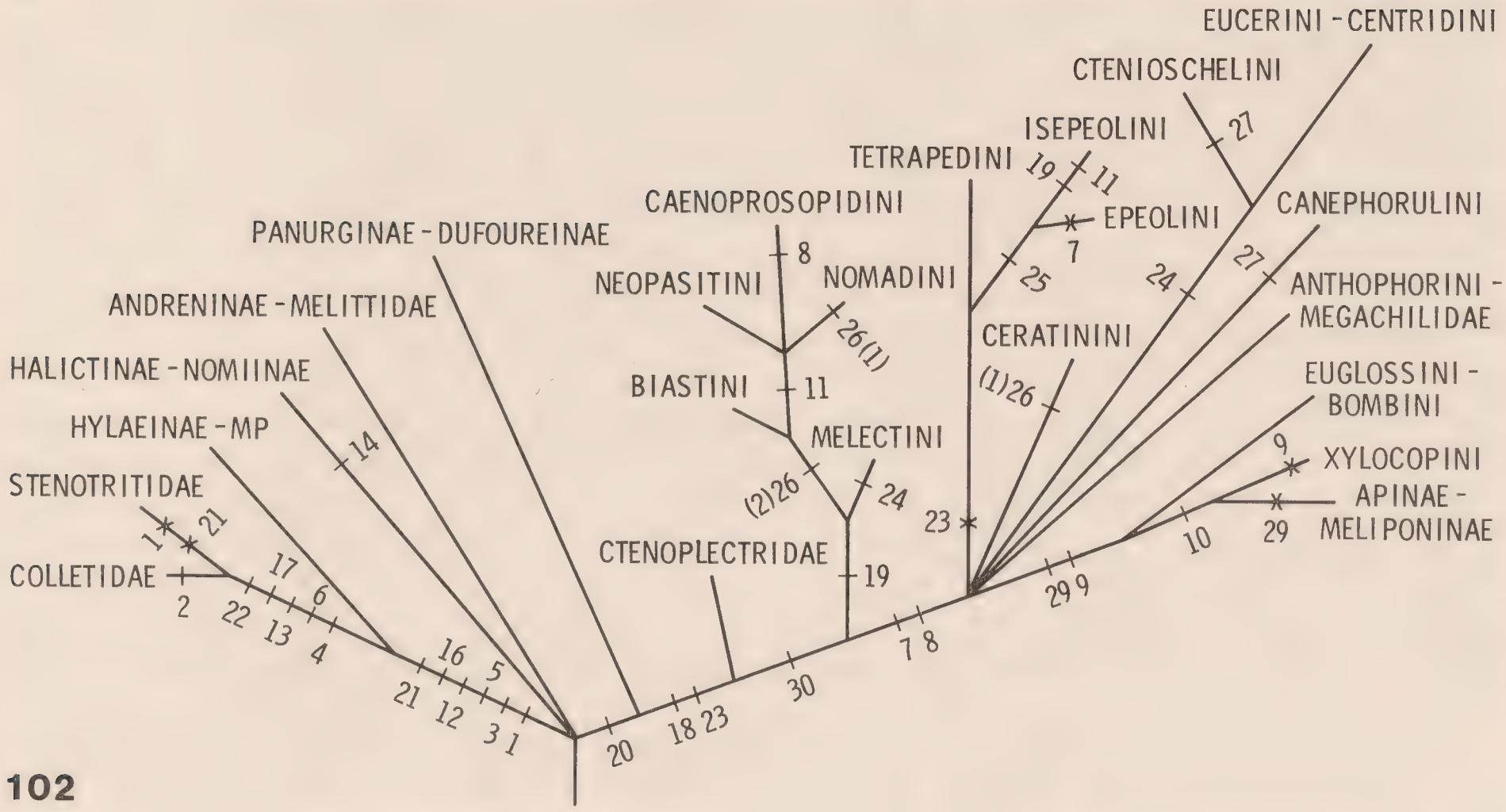
names of family-group taxa does not indicate a broader survey of genera and species. Taxa for which data are incomplete were omitted. There are too few glossal variables with known polarity to make this summary a reliable cladistic pattern for bees. It should be seen as a device for making a body of glossal data more easily accessible and for promoting discussion of some interesting problems. Unfortunately the many fascinating characters of the flabellum exhibit much convergence and it is difficult to determine the polarities of the variables. Therefore the cladistic pattern for long-tongued bees as presented here is not very useful.

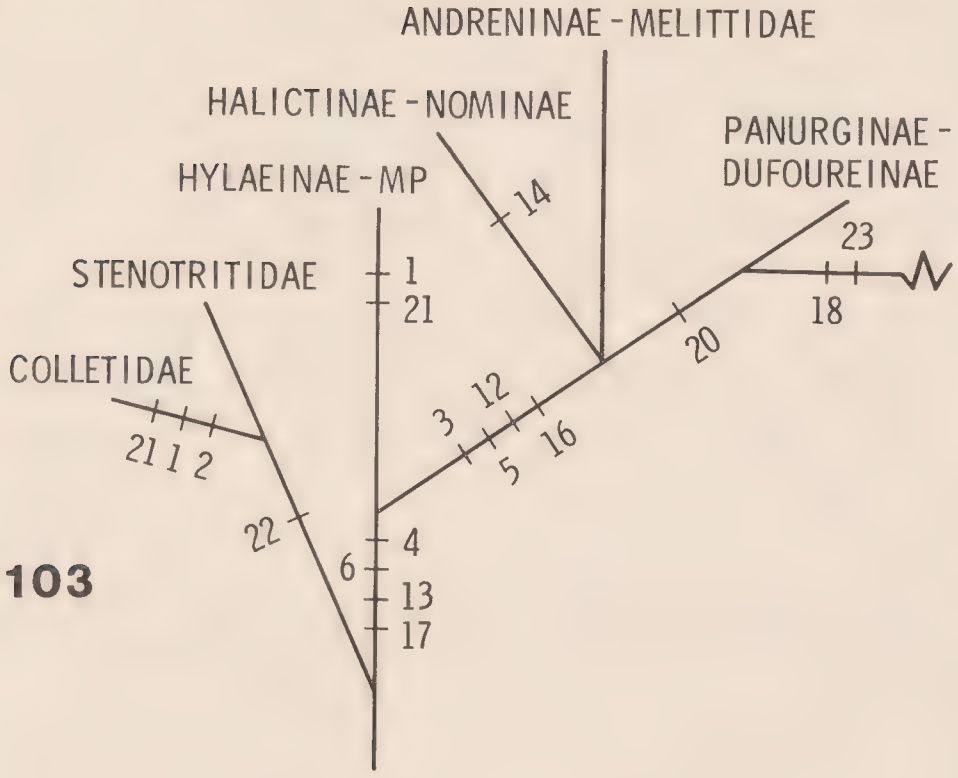
The variables used include some that are almost duplicates. These result from the major sexual differences in several glossal features in the genera Meroglossa and Paleorhiza of the Hylaeinae (Colletidae), so that the females and males would be placed in different families on the basis of glossae if they were not known to be conspecific. One "taxon" included in the study is Hylaeinae-MP, the letters referring to the two genera mentioned which are distinguished from all other colletids by the Andrena-like male glossa. There are six pairs of variables recorded separately for females and males (Table 1) because of this situation, as follows: 1, 2; 3, 4; 5, 6; 12, 13; 16, 17; and 21, 22. In each pair the first is for females, the second for males. The cladograms in Figures 102 and 103 are based on all characters but Figure 104 is based on female characters only, to correct the over weighting of some characters that results from treating them separately for each sex.

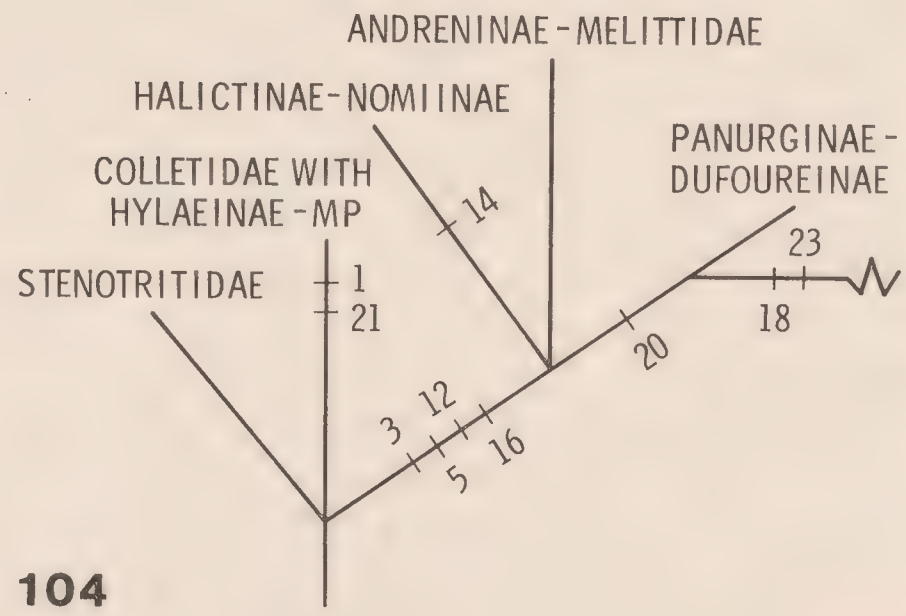
On the cladograms, autapomorphies are omitted. A character is shown on the stem leading to a single taxon if the character appears elsewhere in the cladogram. In Figures 103 and 104 the right hand portions of the cladogram, representing the Ctenoplectridae and long-tongued bees, are omitted since they are similar to the comparable part of Figure 102.

A feature of all the cladograms is the numerous characters isolating the Colletidae and Stenotritidae from the rest of the bees. Elsewhere the number of characters on any given stem is small. An interesting feature is the branch leading to several parasitic groups, the Melectini and various nomadine tribes. The position and content of this branch result from loss of characters like 19 and 26, and from secondary loss of characters 7 and 8 such that apomorphies (losses) within long-tongued bees look like (and for the cladogram are interpreted as) plesiomorphic characters of bees as a whole.

The Colletidae requires attention because the family has been recognized principally on the basis of its glossal shape. This family has traditionally (e.g., Michener, 1944) been regarded as the most primitive family of bees, largely because of the broad and commonly bilobed glossa, sometimes merely truncate or rounded at the apex. This shape resembles that of many other Hymenoptera including the sphecoid wasps from which bees quite clearly arose. The southern distributions of most colletid groups (Michener, 1965, 1979), suggestive of the disjunct southern ranges of many primitive groups of organisms, together with the possession of other (i.e., nonglossal) plesiomorphies, also support the idea that colletids may be the most primitive bees. They could be the sister group of all other bees, or a paraphyletic group from which other bees arose.







Figures 102-104. Cladograms based upon glossal characters of both sexes. Character numbers and polarities correspond with those in Table 1; those indicated by an X are reversions. Autapomorphies are omitted. 102. Cladogram for all higher taxa. The out-group used was all plesiomorphies, a condition also found in the Andreninae-Melittidae. "Colletidae" includes all subfamilies, even Hylaeinae other than Hylaeinae-MP (Meroglossa, Palaeorhiza). "Andreninae-Melittidae" includes also Oxaeidae. "Anthophorini-Megachilidae" includes also Fideliidae, Exomalopsini and Melitomini. These taxa do not differ in the characters here analyzed. 103. Basal part of above cladogram. Polarities are reversed to correspond with "traditional" views for characters 3, 4, 5, 6, 12, 13, 16, and 17 (see text). The out-group was all plesiomorphies, a condition found in some Sphecidae. 104. Basal part of above cladogram based on glossal characters of females only. Explanation as for Figure 103.

Perkins (1912) and McGinley (1980), however, cast doubt on the traditional idea that an obtuse glossa is primitive among bees, and suggested that the acute glossa of certain male colletids (Meroglossa and Paleorhiza) may be more primitive, with the obtuse or bilobed glossa being a "special development" in the words of Perkins. According to this view the most primitive bees must have had a short, acute glossa like most short-tongued bees. Female colletids then evolved a broad, obtuse glossa, presumably in connection with their use of the glossa to paint their distinctive lining material onto the cell and sometimes the burrow walls. Males initially would have retained an acute glossa and two genera still do, but perhaps because the acute glossa had no special advantages for males and required maintenance of separate genetic machinery, it disappeared in most male colletids. According to this idea the obtuse or bilobed glossa is an apomorphy among bees, a superficial reversion toward the ancestral sphecoid glossa. Like Michener (1981), we have accepted this view and elaborated on it in determining the polarity of the characters listed in Table 1 and in preparing Figure 102.

It seems clear that the Colletidae have certain glossal apomorphies at the family level. These are the glossal lobes (1 and 2, Table 1), the glossal brush which is on the lobes and is not separately listed in Table 1, and the preapical fringe (21 and 22, Table 1). These characters are not found in sphecoid wasps nor in any other family of bees. Although lacking in the males of the Hylaeinae-MP group, these characters indicate that the Colletidae is a holophyletic unit, presumably the sister group to most or all other bees, and not a paraphyletic unit from which other bees arose. (Of course the colletid apomorphies could have been lost in the evolution of all other bees, making Colletidae paraphyletic, but this seems improbable.) The colletid apomorphies do not establish by themselves whether the truncate or emarginate glossa of typical colletids is derived from an acute apoid glossa or from a truncate or emarginate sphecoid glossa.

The typical colletid glossa, even without the glossal lobes, is blunt, truncate, or emarginate (3 and 4, Table 1). This shape, according to the Perkins-McGinley view, has been derived from the acute glossa like that found in Andreninae or Halictinae. The shape could have arisen as the base for supporting colletid apomorphies, glossal lobes and the preapical fringe (1, 2, 21, 22, Table 1). This all makes good sense when one postulates, as suggested above, that the colletid glossa arose as a correlate of nest construction by females, leaving males at first (as in Hylaeinae-MP) with acute glossae.

To accept the traditional view that the typical colletid glossal shape is ancestral and that acute glossae arose from it requires that in ancestors of Hylaeinae-MP, an acute glossa evolved first in males, and later became characteristic of both sexes as in Andreninae, Halictinae, etc. This idea is hard to accept because the male glossa has no known special function differing from that of the female. It is the female's glossa that has a special function in nest construction, unlike that of the male. It is for these reasons that for variables 3 and 4, Table 1, we list the pointed glossa as plesiomorphic (for bees; of course it is an apomorphy among Hymenoptera or looked at from the condition of sphecoid wasps).

This view of polarity in variables 3 and 4 is not without problems, however. There are three other morphologically and probably functionally independent variables that are distributed among taxa in the same way as 3 and 4, i.e., the sphecoid features are found in the colletids except for males of Hylaeinae-MP, while the latter and other bees (except Stenotritidae) have the alternative features. These variables are (a) the extent of the annulate surface on the posterior glossal surface (5, 6, Table 1), (b) the shape of the annular hairs (12, 13, Table 1), and (c) the scattered vs. seriate positioning of the disannular hairs (16, 17, Table 1). It is not legitimate to assume reversion in glossal shape to the colletid form from an acute antecedent unless one also accepts the reversion in the other three variables. We have accordingly coded the three other variables also as though they reverted in colletids to the sphecoid condition, i.e., the apomorphies among bees look the same as the plesiomorphic conditions in sphecoids. We emphasize here the gross difference in nearly every attribute between male and female glossae of Meroglossa and Palaeorhiza (Figs. 19 and 20). The male structures can easily be compared and the parts homologized with those of most short-tongued bees while the female glossa is like that of other colletids.

We are faced with two improbabilities--(a) evolution of an acute glossa (and the three accompanying features) first in males, later to be transferred to females, or (b) parallel reversion of four different characters in colletids from bee-like to sphecoid-like. The correct choice may become evident later. For the present, however, we leave the question open. We reversed the coding of characters 3, 4, 5, 6, 12, 13, 16, and 17 (really only four characters if one ignores the sexual differences in Hylaeinae-MP) and made an alternative cladogram (Fig. 103) based on the traditional view that colletid characters are mostly plesiomorphic. This diagram seems to be as informative as Figure 102, although different. Figure 104 is based on female characters only, coded traditionally, and sidesteps the Hylaeinae-MP problem. The cladogram based on female characters only, coded as in Table 1, had a branching pattern like that of Figure 102. Of course a cladogram based on male characters only would put Hylaeinae-MP entirely away from the Colletidae and with the Andreninae.

The endemic Australian family Stenotritidae is important in this connection. It has the colletid glossal characters (3, 4, 5, 6, 12, 13, 16, 17) except for the obvious apomorphies, 1, 2, 21, 22 (Table 1). Thus its glossa could be similar to the type from which the typical colletid glossa evolved. If this were true, one would have to accept the traditional view and believe that the pointed glossa and associated features arose first in males.

Given the fact that males of a few colletids have glossae that are in all features like those of acute-tongued, noncolletid, short-tongued bees, one may expect to discover bees that are in most features colletids, but that have acute glossae in both sexes, or at any rate glossae that are not of the usual colletid style. Possibly such bees should be included in the Colletidae, since obviously the colletid-style glossa is not an essential feature of the family, at least in males. Candidates for possible inclusion in the Colletidae are the Oxaeidae and Stenotritidae. This idea is attractive because of the similarity of

these families in various features to the colletid subfamily Diphaglossinae.

TABLE 1

Synapomorphies (with corresponding plesiomorphies in parentheses) for some glossal characters of bees. Numbers in parentheses refer to paragraphs where the characters are more fully explained. For variable 26, two supposedly sequential, derived characters are indicated by the numbers 1 and 2. Variables 15 and 28 are purposely omitted since they were autapomorphic.

1. Glossa of female with glossal lobes so that it is truncate or bilobed (1.2, 6.2).
   (Glossa of female without glossal lobes. Glossal lobes are absent in Sphecidae.)
2. Glossa of male with glossal lobes so that it is truncate or bilobed (1.2, 6.2).
   (Glossa of male without glossal lobes. Glossal lobes are absent in Sphecidae.)
3. Glossa of female (excluding glossal lobes if present) rounded, truncate, or emarginate at apex (1.2).
   (Glossa of female pointed. See Discussion.)
4. Glossa of male (excluding glossal lobes if present) rounded, truncate, or emarginate at apex (1.2).
   (Glossa of male pointed. See Discussion.)
5. Annulate surface of female entirely or almost entirely on anterior side of glossa (2.1).
   (Annulate surface of female curling onto posterior surface of glossa. See Discussion.)
6. Annulate surface of male entirely or almost entirely on anterior side of glossa (2.1).
   (Annulate surface of male curling onto posterior surface of glossa. See Discussion.)
7. Disannulate surface of glossa largely hidden (invaginated) (2.2, 2.3, 4.1).
   (Disannulate surface of glossa exposed, as in Sphecidae.)
8. Glossal rod present (4.4, 4.5).
   (Glossal rod absent, as in Sphecidae.)
9. Glossal rod appearing double (4.5).
   (Glossal rod absent or if present appearing simple. The rod is absent in Sphecidae and many bees, and is not double in most bees that have a rod.)
10. Bacular canal nearly closed (4.5).
    (Bacular canal absent or wide open. There is no such canal in forms that lack a rod, as well as in most forms that have a rod.)
11. Margins of disannulate surface with thin, broad lamellae (3.2).
    (Margins of disannulate surface without lamellae. Such lamellae are present only in a few otherwise strongly apomorphic bees.)
12. Annular hairs of glossa of female minute, short, blunt or capitate (3.1, 3.3).

(Annular hairs of glossa of female elongated, ending in one or more points.See Discussion.)

13. Annular hairs of glossa of male minute, short, blunt or capitate (3.1, 3.3).
(Annular hairs of glossa of male elongate, ending in one or more points.See Discussion.)

14. Annular hairs of glossa, or some of them, divergently branched preapically (3.4).
(Annular hairs not branched, as in Sphecidae and most bees.)

16. Disannular hairs of female scattered (5.1-5.10).
(Disannular hairs of female in two rows (the seriate hairs), or sometimes absent.See Discussion.)

17. Disannular hairs of male scattered (5.1-5.10).
(Disannular hairs of male in two rows (the seriate hairs), or sometimes absent.See Discussion.)

18. Disannular hairs convergent, seriate, rarely absent (5.1-5.10).
(Disannular hairs divergent and seriate, or scattered, rarely absent.See Discussion.)

19. Disannular hairs absent (5.10).
(Disannular hairs present.Such hairs are present in Sphecidae.)

20. Glossa with apical specialization (not including glossal lobes of Colletidae) (6.5).
(Glossa without apical specialization, as in Sphecidae and many bees, or with apical lobes in Colletidae.)

21. Glossa of female with a preapical fringe (1.2).
(Glossa of female without a preapical fringe, as in Sphecidae.)

22. Glossa of male with a preapical fringe (1.2).
(Glossa of male without a preapical fringe, as in Sphecidae.)

23. Flabellum present (7).
(Flabellum absent, as in Sphecidae and many bees.)

24. Posterior surface of flabellum cobblestoned (7.14, 7.15).
(Posterior surface of flabellum not cobblestoned or flabellum absent.)

25. Apical specialization or flabellum with setae on posterior as well as anterior surface (7.10, 7.11).
(Apical specialization or flabellum without setae or flabellum absent.This is as in Sphecidae and nonparasitic bees.)

26. (1) Flabellum reduced so that setae basal to flabellum arise near its apex but a zone of disannular hairs is present on anterior surface between setae and apex (7.8).
(2) Flabellum more reduced, so that no zone of disannular hairs intervenes between setae basal to flabellum and its apex (7.9).
(Flabellum without setae seeming to arise near its apex, or flabellum absent. Sphecidae and many bees lack a flabellum. Among bees that have one, a widespread and presumably plesiomorphic pattern is a flabellum extending far beyond its base and with a large anterior surface occupied by hairs.)

27. Setae arising on anterior surface of flabellum proper (7.13).

(Setae, if present, basal to flabellum, if present. This is as in nearly all bees.)

29. Elongate, preflabellar, nonannular, hairless zone present (7.17).
(No such hairless zone, the flabellum, if present, arising from apex of hairy part of glossa, as in nearly all flabellate bees.)

30. Basiglossal sclerite rather long with a pair of posterior basal processes (hence the term bonnet-like sclerite).
(Basiglossal sclerite a transverse ribbon or band, as in Sphecidae.)

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